University of Alberta

A Study of Geographic and Genetic Variation of Scots Pine (*Pinus sylvestris* L.) in Alberta.

by

Deogratias M. Rweyongeza ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements of the degree of Master of Science

in

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Rweyongeza

National Tree Seed Centre
P. O. Box 4012
Morogoro, TANZANIA

Date 12 February 1997

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the faculty of graduate Studies and Research for acceptance, a thesis entitled A Study of Geographic and Genetic Variation of Scots Pine (*Pinus sylvestris* L.) in Alberta submitted by Deogratias M. Rweyongeza in partial fulfillment of the requirements of the degree of Master of Science in Forest Biology & Management.

Bruce P. Dancik

Bruce P. Dancik
Co-supervisor

Francis C. Yeh
Co-supervisor

Jack Heidt

Jack D. Heidt

NKDhir

Narinder K. Dhir

Robert T. Hardin

Robert T. Hardin

Date February 7, 1997

TO MY WIFE **ESTHER** AND MY DAUGHTER **LUCIA**

ABSTRACT

This study involved seven Scots pine populations from Siberia, Russia. It was conducted on three sites in Central Alberta. Assessment included height, diameter, branch and needle lengths. At six years, the population variance was less than 5% and 1% of the total variance on individual and across sites, respectively. The family variance was less than 9% and 3% of the total variance on individual and across sites, respectively. The Genotype by environment interaction in heights was high. Individual tree heritabilities were less than 0.35 and 0.15 at individual and across sites respectively. Family heritabilities were between 0.13 and 0.60, and 0.24 and 0.62 on individual and across sites, respectively. Genetic and phenotypic correlations were high. Further testing with many populations and families, and more assessment of the existing trials is recommended.

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LIST OF ABBREVIATIONS

DF - Degrees of Freedom

EMS - Expected Mean Squares

Fam - Family

GLM - General Linear Models

G x E - Genotype by Environment

IUFRO - International Union of Forest Research Organizations

HIGH. - Highest

LOW. - Lowest

MS - Mean Squares

NID - Normally Independently Distributed

Pop - Population

PROC VARCOMP - Variance Components Estimation Procedure

Rep - Replication

RSFSR - Russian Soviet Federative Socialist Republic

1. INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

Scots pine is the most important timber species in northern Europe and parts of Asia where it occurs in abundance. It is less important in southern Europe where it occurs in isolated patches (Wright and Bull 1963). Scots pine produces high quality wood under favourable cultural conditions, and tolerates a wide range of climatic conditions (Carlisle and Brown 1968). In north-central USA and Canada, Scots pine is an important Christmas tree species (Wright and Bull 1963; Van Haverbeke and Gerhold 1991; Giertych 1991). A study by Knopf and Wall (1992) showed that Scots pine was more economically viable for Christmas trees in Saskatchewan than white spruce (*Picea glauca* (Moench) Voss), white pine (*Pinus strobus* L.), and balsam fir (*Abies balsamea* (L.) Mill). This is due to its higher growth rate than the other three species. In later sections, it will be shown that Scots pine also has potential for timber production in Canada that justifies genetic research for its effective utilization.

Every tree breeding programme for both native and introduced species generally requires a range-wide provenance test before proceeding with breeding work. The objective is to make use of improvements already made in the wild by natural selection (Wright 1976). By skipping a provenance test, a breeder risks selection and breeding from inferior populations to achieve improvements that would likely have been attained by simply introducing superior populations based on provenance test results. Provenance tests are also important in exploring variation trends and linking them with environmental factors. They are therefore important in evolutionary studies (Wright 1976).

Equally important is a progeny test. Breeders need progeny tests to estimate the amount of genetic variation within populations, and genetic parameters such as heritability and breeding values of the genetic lines. Since selection is always done on the phenotype rather than the hidden genotype, heritability guides the breeders in deciding the appropriate selection method to optimize genetic gains (Falconer 1960). Selection methods that do not take the population structure into consideration may lead to reductions in genetic gain, and wastage of resources.

In Scots pine, several provenance and progeny tests have been done in Europe and North America (especially the United States). However, there have been only a few such studies in Alberta where Scots pine is considered an alternative species for afforestation (Dhir et al. 1989). The current study on the geographic and genetic variation of Scots pine in Alberta is an attempt to gather basic information for possible formulation of a Scots pine breeding programme in the province. Because of previous experience (see section 1.2.4), this study focuses exclusively on Russian provenances.

Scots pine is an exotic species in Alberta. For better understanding of the species, this thesis includes a literature review on provenance and progeny studies conducted in and outside Canada. The main objective of this thesis is to cover the provenance and progeny study of Scots pine established in the province in 1988. Comparison of Scots pine with local Canadian pines is out of the scope of this thesis. The thesis discusses in details, the practical implications of the observed levels of genetic variation and genetic parameters to provenance introduction, and selection and breeding of Scots pine in Alberta. Also, it provides recommendations on long term research needs.

1.2 Literature Review

1.2.1 The Species

In botanical terms, Scots pine is known as *Pinus sylvestris* L. Taxonomically, it belongs to the family *Pinaceae*, subgenus *Diploxylon* (pines with 2 sometimes 3 vascular bundles in needles) and sections *Eupityl*, the most numerous section in the genus *Pinus* (Malotkov and Patlaj 1991). Following many provenance studies in Europe and North America, there have been attempts to divide the species into subspecies and varieties (Staszkiewicz 1975; Wright and Bull 1963; Ruby and Wright 1976). Ruby and Wright (1976) provide the most recent and detailed description of possible Scots pine varieties.

Whether Scots pine is divisible into subspecies and varieties or not is out of the scope of this thesis. Studies have shown that subdivisions of Scots pine do not apply in places like Sweden (Gullberg et al. 1985), although scientists like Ruby and Wright (1976) proposed varieties for this region based on provenance studies conducted in the United States. Some scientists have criticized the whole idea of subdividing Scots pine into subspecies and varieties. Giertych and Oleksyn (1981) for example argued that the proposed varieties are simply climatic races rather than varieties in the real meaning of the word. To avoid taxonomic misrepresentation, Scots pine in this thesis will be treated as a species with no taxonomic subdivisions. Furthermore, grouping of Scots pine into ecotypes, which is a common idea in Scots pine literature (see, e.g., Wright and Bull 1963) will be avoided. In subsequent sections, provenances will be referred to by places of origin rather than the varieties and ecotypes in which they may be assumed to belong.

1.2.2 Geographic Distribution of Scots Pine

Scots pine is the most widely distributed pine species in the world (Boratynski 1991). If outlier populations are included, its natural range extends from the seas of Okhotsk and Japan to the Atlantic ocean, and from Barrents sea to the Mediterranean sea (Bialobok 1975). Horizontally, it traverses 33° of latitudes (2700 km), from 37° 00' N in Sierra Nevada, Spain, to 70° 20' N in Norway, and 133° of longitudes (14000 km), from 8° 00' E in Spain to 141° 00' E in the Soviet Far East (Boratynski 1991).

Scots pine is, however, not found everywhere across Europe and Asia (Figure 1). Specifically, its natural range extends from western-central Spain through France, northern Italy, southern Germany, Turkey, Scotland, Norway, Sweden, Finland, across eastern Europe to the Soviet Far East (Wright and Bull 1963; Boratynski 1991). In Belgium, the Netherlands, Denmark, England, and northern Germany, Scots pine is not native. Its presence in these areas is due to introductions in past centuries (Giertych 1979; Heybroek 1974; Wright and Baldwin 1957; Wright et al. 1966). Its range is continuous over large parts of Scandinavia, northern Russia, Siberia, and central Europe. It has a broken distribution in France and Italy, whereas in Spain and Turkey it occurs in scattered stands (Wright and Bull 1963).

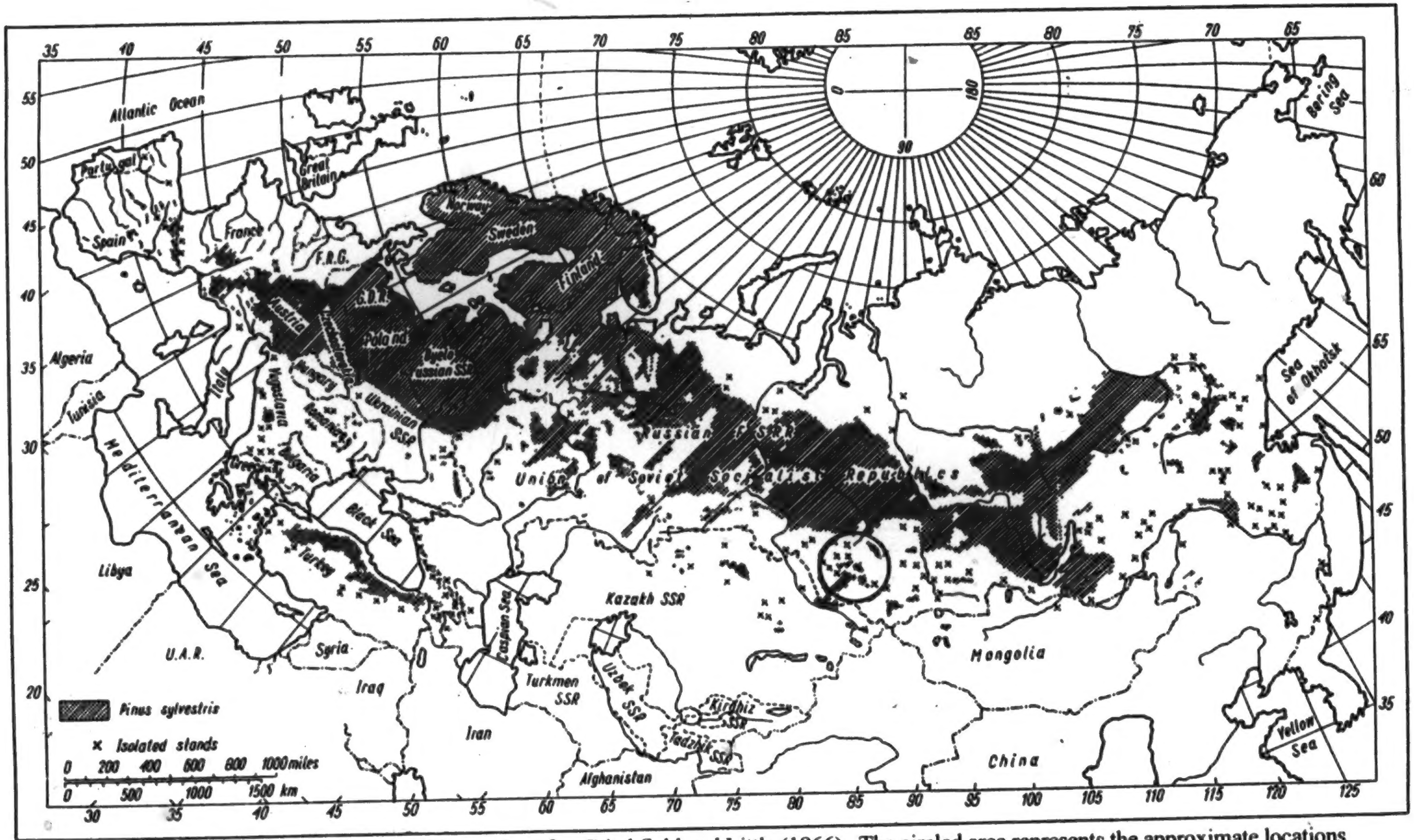

Figure 1: Natural geographic distribution of Scots pine after Critchfield and Little (1966). The circled area represents the approximate locations of the populations used in this study.

Scots pine has also a wide range of elevation in its natural range. The highest altitude reached in the Caucasus mountains is between 2500 and 2600m above mean sea level (a.s.l.), although some dwarf solitary trees can be found at 2700m (Boratynski 1991). In Sierra Nevada, Spain, Scots pine occurs at altitudes as high as 3110m a.s.l. (Bialobok 1975). Scots pine also occurs at much lower elevations, e.g., 277m a.s.l. in Maldalen, Scandinavia (Bialobok 1975).

1.2.3 Geographic and Genetic Variation in Scots Pine

1.2.3.1 Geographic Variation

1.2.3.1.1 Previous Provenance Studies

Because of its very wide distribution in terms of latitudes, longitudes and elevation, Scots pine is expected to show greater geographic variation than other pines. With such a wide distribution, the species inhabits a variety of soils, moisture regimes, day and night length (photoperiod), and temperature extremes. According to Obminski (1975), Scots pine is found in areas with temperatures as low as -40°C in winter to those with hot summers of up to 35°C. This section reviews the findings of various provenance studies in Scots pine conducted in Europe and North America for approximately one hundred years.

The first study of geographic variation in forest trees was done with Scots pine in France as early as 1820 (Wright and Bull 1963). Following the revelation that trees from different sources could grow at different rates and differ in quality traits, many provenance studies have been done in Scots pine both in and outside its natural range. Major provenance studies includes: (1) those organized by the International Union of Forest Research Organization (IUFRO) in 1907, 1938, 1939 and 1982 in Europe and North America (Giertych 1975, 1979 Giertych 1991), (2) the NC 51 (later NC 99) series under the title "Tree Improvement Through Selection and Breeding of Forest Trees of Known Origin" in the United States (see, e.g., Wright and Bull 1963; Wright et al. 1966; Steinbeck 1966; Tobolski and Hanover 1971 and Ruby and Wright 1976), and (3) the Ogievskij's series which include all provenance studies in pre-revolutionary Russia (Giertych and Oleksyn 1992). Similar studies have been done on a regional and individual country basis, e.g., in Scandinavia, USA and Canada.

1.2.3.1.2 Geographic Variation of Some Common Traits

Most of the range-wide provenance studies in Scots pine concentrated in studying morphological variation especially in growth, quality, needles and phenological traits. From these studies the following general conclusions can be made.

(i) Variation in Growth Traits

In terms of growth potential (height, diameter, volume), the best provenances are those from Baltic countries and north Poland (Giertych 1979, 1991; Oleksyn and Giertych 1984; Giertych and Oleksyn 1992; Ruby and Wright 1976), and northwest Germany, Belgium, the Netherlands, north Italy and northern France (Giertych 1979; Wright and Bull 1963). Provenances from Hungary, Czechoslovakia, parts of Germany and Poland were also fast growing. Scottish provenances and those from southern Scandinavia showed average growth, whereas those from northern Scandinavia and outlier populations from north and south of the species natural range showed poor growth (Wright and Baldwin 1957; Giertych 1979, 1991). Provenances from the western part of Russia showed greater growth, whereas those from the northern part showed poor growth (Mikhal'chenko 1989; Kotov 1989; Redko 1989; Giertych and Oleksyn 1981). Saatcioglu (1967) suggested that the best provenances in terms of growth originate from the lowlands of central Europe between latitudes 45° N and 55° N. Provenances from this region showed the best growth in almost all places they were tested, both in Europe and North America. Provenances from outside this region were either average or poor in growth.

Connected to growth rate, is variation in the root system. The fast growing central European provenances showed a poorly developed taproot but generally balanced root system in terms of root branching. Northern provenances showed a developed taproot with limited lateral roots, whereas provenances from southern Europe had a very developed taproot with less branched lateral roots (Wright and Bull 1963; Brown 1969). A strong taproot system in provenances from southern Europe is considered an adaptation to moisture stress that characterize the region (Wright and Bull 1963). Wright and Bull also considered a strong taproot system in provenances from northern Scandinavia an adaptation to low temperature that could cause tree mortality through frost heaving (Wright and Bull 1963).

(ii) Variation in Quality Traits

Provenance studies showed opposing geographic trends between growth and quality traits in Scots pine. All major studies showed that the fastest growing provenances from central Europe produced crooked stems, whereas the slowest growing provenances from northern Scandinavia produced straight stems (Wright and Baldwin 1957; Giertych and Oleksyn 1992; Saatcioglu 1967). Provenances from northern Sweden produced straighter stems with fewer spike knots than provenances from southern Sweden (Prescher and Stahl 1986). In New Hampshire, USA, the fastest growing provenances from central Europe produced the thickest branches, whereas the slowest growing provenances from Scandinavia produced the thinnest branches (Wright and Baldwin 1957). In Sweden, Eriksson et al. (1987) found that branch diameter was positively correlated with latitudes of seed origin. Southward transfer of provenances would reduce the branch diameter.

The opposing trends between growth and quality traits means that one cannot jointly optimize growth and product quality through provenance transfer alone. Since fast growing and well-adapted provenances from central Europe will likely contain both straight and crooked individuals, Scots pine can be improved by first introducing the best provenances from central Europe to secure adaptation, and then select straight trees to improve quality.

(iii) Variation in Foliage Characteristics

The size and colour of needles have been useful traits in studying geographic variation in Scots pine. In Michigan, the fastest growing provenances from central Europe also had the longest needles (Wright and Bull 1963; Ruby and Wright 1976). Unexpectedly, Spanish provenances, which grew faster than Scandinavian provenances, had the shortest needles (Ruby and Wright 1976). This suggests lack of direct relationship between growth rate and needle length (Wright and Bull 1963). In Turkey, Saatcioglu (1967) found that needles were the longest (> 70.00mm) in provenances from central Europe, intermediate (50.00 - 65.00 mm) in Scottish, Romanian, French and some Norwegian provenances, and the shortest (<

50.00mm) in provenances from southern Scandinavia.

Needles of Scandinavian provenances turned yellow in winter (Saatcioglu 1967), whereas those of the Spanish and Turkish provenances remained dark-green in both winter and summer (Wright and Bull 1963; Wright et al. 1966; Ruby and Wright 1976). Maintenance of green needles in winter is an important attribute for Scots pine to serve as a Christmas tree species. This is important especially in north-central USA and Canada where Scots pine is widely used for Christmas trees. In Michigan for example, Christmas tree growers prefer Spanish Scots pine provenances because of their permanent green colour (Wright et al. 1966).

(iv) Variation in Cone and Seed Characteristics

Cone and seed characteristics are widely used in identification of species, varieties, races, and in studying hybridization and introgression among species (Ruby 1967; Wheeler and Guries 1986). The north-south trend in seed size variation exists in Scots pine. Provenances from northern Scandinavia produce the smallest seeds, whereas the southernmost provenances from Turkey and Spain produce the largest seeds (Ruby 1967; Wright and Bull 1963). Karrfalt et al. (1975) found that Russian and Spanish provenances produce heavier seed than provenances from other regions.

Reich et al. (1994) found that seed size / weight was strongly correlated with the latitude of seed sources. The smallest seeds belong to provenances from north of latitude 60°N, whereas the largest seeds belong to provenances from south of latitude 50°N. Exceptions from this general trend were English provenances, which produced larger seed than expected from their latitudes of origin. English Scots pine is of plantation origin, possibly a hybrid of

Scottish and Germany provenances (Ruby 1967). Thus, exceptionally large seed in English provenances of Scots pine may be an indicator of hybrid vigour (Ruby 1967). Wright et al. (1966) and Park and Gerhold (1986) observed similar hybrid vigour in Scots pine for height and diameter. Ruby (1967) considered large seeds of provenances from southern Europe, an adaptation to moisture stress. In these areas, only trees with large seeds that could germinate and send roots deeper in the soil could survive.

Except English populations, cone size in Scots pine showed a north-south variation. The smallest cones came from provenances north of the Arctic cycle, whereas the largest cones came from Spanish and Turkish provenances (Ruby 1967). Cone size variation is expected to follow seed size variation, since large cones may be needed to carry large seeds and vice versa.

(v) Variation in Phenology

Phenology is the study of the timing of a plant's periodic biological phenomena such as budsetting, leaf flushing, flowering, fruit formation, fruit maturity and seed / fruit dispersal (Wright 1976). Phenology has been a subject of intensive study in Scots pine, and geographic trends have been established. In Michigan, most of the provenances from northern Europe formed winter buds in the middle of July, whereas Spanish provenances formed buds in late October (Wright and Bull 1963). Mikola (1982) found that in Finland budsetting was strongly correlated with the latitude of seed origin and the number of degree days, i.e., number of days with temperature above 5°c. Here, provenances from around 70°N formed buds in early July, those around 65°N formed buds in mid-July and early August, whereas those around 60° N formed buds in early September.

Early and late cessation of shoot growth of northern and southern provenances, respectively, is not unexpected since the two provenance groups are adapted to growth periods of different lengths. With fewer warm days and thus shorter growth periods, northern provenances should cease shoot growth earlier than southern provenances. On the contrary, southern Europe has many warm days and thus, a longer growth period than northern Europe. Therefore, provenances from southern Europe are expected to cease shoot growth later than provenances from northern Europe.

The formation of Lammas shoots, i.e., shoots formed in midsummer from normally formed buds after some period of rest (Wright and Bull 1963; Przybylski 1975; Wright 1976), was common in provenances from Turkey, Greece, France and Spain (Wright and Bull 1963). Wright and Bull (1963) suggested that formation of Lammas shoots in southern provenances might be a trait selected for late maturation. This would, however, not explain the existence of Lammas shoots in the French provenances.

(vi) Variation in Survival and Frost Tolerance

Tolerance to frost and moisture stress is a character directly linked with survival of the species especially in an exotic environment. Kotov (1989) observed that Scots pine provenances from high latitudes exhibited greater frost tolerance than provenances from lower latitudes. Consequently, northward transfer of provenances resulted in reduced survival, whereas southward transfer increased survival. In Sweden for example, Persson and Stahl (1990) found that while northward transfer decreased survival, southward transfer by 1° of latitude increased it by 7.5%. Eiche and Anderson (1974) also reported poor survival of provenances from southern Sweden when transferred to northern Sweden.

Eriksson et al. (1987) found that provenance survival was more influenced by changes in latitudes of seed origin ($r^2 = 0.77$) than the changes in elevation of seed origin ($r^2 = 0.14$). The limitations of elevation in producing frost tolerant strains deserves a brief discussion. Theoretically, a change of 1000 metres in altitude can produce climatic changes similar to those produced by a change of hundreds of kilometres in latitudinal distance (Wright et al. 1971). However, changes in altitudes involve shorter physical distances than the equivalent changes in latitudes. Thus, the possibility of gene flow among populations on elevational gradients is much higher that among populations on latitudinal gradients (Wright et al. 1971). Consequently, the rate of population differentiation on elevational gradients is much lower than on latitudinal gradients.

High frost tolerance of provenances from high latitudes is understandable since temperature decreases with increases in latitudes. Consequently, high latitude seed sources are naturally selected for lower temperatures than low latitude seed sources. This difference in selection should be reflected in their survival when transferred outside their natural environment, where temperature is the determining factor of survival.

(vii) Variation in Pest and Disease Resistance

Pests and diseases are frequently encountered problems when trees are managed in pure plantations, especially in exotic environments (Zobel and Talbert 1984; Zobel et al. 1987). Scots pine has a considerable resistance to various pests and diseases in and outside its natural environment. In Sweden, northern and inland provenances showed greater resistance to snow bright fungus (*Phacidium infestans* Karst) than provenances from the south and coastal areas (Bjorkman 1963). Fungal resistance was linked with the amount of organic matter in the plant tissues (Bjorkman 1963; Ladejshikova et al. 1989). According to Ladejshikova et al. (1989), one can identify Scots pine trees resistant to *Heterobasidion annosus* in Russia by the type and amount of organic and inorganic substances in the tissues.

In Michigan, provenances from central Europe were more susceptible to pine fly (*Neodiprion sertifer* Geoff.), white pine weevil (*Pissodes strobi* Peck) and jack pine budworm (*Chloristoneura pinus* Freeman) than provenances from extreme north and south of Scots pine range (Wright et al. 1966). Provenances from north and central Europe were resistant to pine webworm (*Tetralopha robustella* Zell.), whereas those from southern Europe were susceptible to it (Wright et al. 1966).

1.2.3.1.3 The Value of Local Provenances

An important goal of provenance testing is to search for populations that are more adapted than local ones (Giertych 1989). An important observation from past provenance tests in Scots pine, is the realization of the value of local provenances. In almost all provenance studies, local populations showed satisfactory growth in studies located close to their places of origin (Giertych 1979, 1989, 1991; Oleksyn and Giertych 1984; Mikhal'chenko 1989; Kotov 1989). For example, in the 1907 IUFRO trials, the Spis and Bratislava provenances did well at the Likavka experimental site nearest to their origin and performed poorly elsewhere (Giertych 1979). In the 1939 IUFRO trials the Turkish provenances did well in the trials located close to their localities. The same provenances were ranked among the poorest outside Turkey in the three IUFRO series. For example, the Catacik provenance from Turkey, suffered complete mortality in Bavaria, Germany, but showed good growth and survival at its locality in Turkey (Saatcioglu 1967). In Canada, the local (possibly adapted land race) provenance near Lake Ontario was among the best provenances in the 1939 IUFRO experiment at Norfolk County, Ontario (Giertych 1979). At Kiruna, Linalombolo and Asplovberg, Sweden, local populations expressed good survival while populations from far distanced were nearly wiped out (Eiche and Anderson 1974).

Populations occurring at any locality, evolve in response to climatic extremes characteristic of that environment. They are therefore likely to be more adapted in terms of drought and frost tolerance, and resistance to pests and diseases than populations introduced from other areas. Thus, introduction of new provenances should be done only when intended improvements can be achieved without compromising adaptation.

1.2.3.1.4 Performance of Outlier Populations

Outlier populations are populations occurring outside the "official" natural range of the species. In Scots pine, outliers are common in places like Scotland, Spain, Turkey, Greece and southern Russia. Generally, performance of these populations was poor in all provenance tests. Because of the good growth and survival of provenances when tested in their localities, Giertych (1991) suggested that outlier populations may be considered poor because very few trials were located in outlier localities. This means that there is very little knowledge about outlier populations compared to populations from the main distribution of Scots pine. Also Giertych (1991) suggested that outlier populations may have suffered genetic drift. According to Wright and Bull (1963), there is evidence to suggest that random genetic drift has occurred in Scotland, Greece and parts of Spain. In Michigan for example, Wright and Bull (1963) observed that branched terminal bud was a character restricted to Scottish populations. Since such a character is unlikely to have adaptive significance, they interpreted it as the result of random genetic drift in small and isolated Scottish populations. Thus, random genetic drift and inbreeding depression that result from long time isolation of small populations may be responsible for the poor performance of outlier populations.

As stated by Giertych (1989, 1991), it is unobjectionable that outlier populations are of no value when transferred, but locally can have value due to their adaptation to the local environment. Although such populations may be desirable for genetic improvement purposes, they are undesirable for genetic conservation because of their possible low genetic variability that makes them vulnerable to extinction.

1.2.3.2 Genetic Variation

1.2.3.2.1 Progeny Testing

Progeny testing is the method of evaluating parents' genetic quality by phenotypic performance of their offspring under a specified set of environmental conditions. It involves creation of progenies, establishment of experiments with a family structure, assessment, statistical evaluation, genetic interpretation, and breeding decisions (Lindgren 1991). Progeny testing can be done by sampling and testing families from the best provenances confirmed to be well adapted in provenance tests. Alternatively, a progeny test can be combined with a provenance test by retaining family identities. The latter approach is the better one as it enables one to identify the best provenances and families simultaneously in the same study. This reduces the time required for research before making breeding decisions and the resources required for research.

1.2.3.2.2 Progeny Testing in Scots Pine

Early studies in Scots pine such as the IUFRO 1907, 1938, 1939, 1982; NC 51 (NC 99); Ogievskij's series and other regional and national studies were exclusively genecological. Their aim was to explore the extent of genetic variation in Scots pine at the regional and population-within-regions levels. Consequently, the extent of genetic control of variation in traits assessed in these experiments could not be established since bulk seedlots were used throughout. Seeds were obtained from research organizations, forest managers, individual contact persons and even commercial seed dealers in Europe who did not keep family identities (Wright and Bull 1963). More important, it would be of little use to test specific families across Europe and North America. This is because progeny tests are designed for selective breeding of economic traits and their results are often specific to target areas of study (Falconer 1960).

In recent years, progeny tests in Scots pine have been conducted mostly in Scandinavian countries, Germany and the United States. These studies provide information on heritability and genetic correlations of some common traits as they apply at respective test sites. However, the results of these studies will not be reviewed in this section. They will appear in later sections when discussing the results of the current study.

1.2.4 Russian Scots Pine in Canada

As mentioned earlier, the main purpose of growing Scots pine in North America is production of Christmas trees. However, Scots pine, especially that of Russian origin, has great potential for uses other than Christmas trees in Canada. In Rich Valley, Alberta, the Russian Scots pine was compared with Scots pine from Scotland and Sweden, ponderosa pine (*Pinus ponderosa* Laws.), jack pine (*Pinus banksiana* Lamb.), and lodgepole pine (*Pinus contorta* Lamb. spp. *latifolia* Englm.). At age 40 years, the Russian provenance from Leningrad outgrew the local pines and other provenances of Scots pine (Kasper and Szabo 1969; Soos and Brown 1970). The wood quality of the Russian Scots pine provenance compared well with that of white spruce (*Picea glauca* (Moench) and lodgepole pine (Kasper and Szabo (1969). Kasper and Szabo predicted that the Russian Scots pine would produce as much wood of the same quality in a 56-year rotation as produced by white spruce and lodgepole pine in an 80-year rotation. In a provenance study in Alberta, the Russian Scots pine population outgrew a lodgepole pine population from approximately the same latitudes, by 35% in height and 50% in diameter (Dhir et al. 1989). The Scots pine population was also hardier to late spring frost than lodgepole pine.

Provenance studies in other parts of Canada, also support the better performance of Russian Scots pine in Canada. In Ontario and Manitoba, Russian provenances performed better than Scots pine from other areas (Klein 1970; Teich and Holst 1970). At Prince Albert, Saskatchewan, the tallest Russian Scots pine provenance outgrew jack pine by 15% in height, and its survival was 76% higher than that of jack pine (Teich and Holst 1970).

The better performance of Russian Scots pine in Canada is linked to environmental similarities between Canada and Russia (Giertych 1975). According to Giertych, the North American continental climate corresponds well with the climate of central Russia. This can promote excellent growth and survival of Russian provenances in Canadian provinces with the continental climate. This is why much of the research in Scots pine in Canada is directed at Russian provenances. Generally, there is much to be gained by Scots pine in Canada both as a timber and Christmas tree species, if appropriate provenances can be identified and deployed in appropriate environments.

2. MATERIAL AND METHODS

2.1 Objectives of the Study

The current research in Scots pine, is part of the wider genetics and tree improvement programme by the Alberta Forest Service (Dhir et al. 1989). It involves species, provenance, and progeny testing. This combined provenance and progeny study has the following objectives:

(1) To assess the potential of Russian Scots pine as an alternative commercial species in Alberta, (2) to estimate the amount of genetic variation between and within-populations, and other genetic parameters for possible developing a breeding programme for Scots pine, and (3) to estimate genetic and phenotypic correlations between traits of Scots pine. This thesis addresses the second and third objectives only. The key questions to be answered in this study are: (1) Is there genetic variation between populations and families within populations in Scots pine? (2) Are different traits in Scots pine correlated genetically and phenotypically? (3) What is an appropriate selection method for improving Scots pine in Alberta? For all traits assessed, the null hypothesis tested was that of lack of genetic variation ($\sigma_x^2 = 0$) among populations or families. The alternative (research) hypothesis was "at least one of the populations or family within populations differs from the rest", i.e., $\sigma^2 > 0$.

2.2 Types and Sources of Test Material

2.2.1 Scots Pine Seedlots

The study involved 30 open-pollinated families grouped into 5 populations, and 3 bulk open-pollinated seedlots of Scots pine from Russia (Table 1). The seeds were obtained by the National Tree Seed Bank, Canadian Forest Service at Petawawa.

Table 1: Scots pine populations used in the study.

POPULATION	LATITUDE (N)	LONGITUDE (E)	NO. OF FAMILIES
1. Kemgrovo, RSFSR, USSR	54° 85'	85° 19'	5
2. Kemgrovo, RSFSR, USSR	54° 00'	86° 20'	10
3. Novosibirsk, RSFSR, USSR	54° 08'	81° 16'	5
4. Novosibirsk, RSFSR, USSR	55° 05'	82° 45'	6
5. Novosibirsk, RSFSR, USSR	54° 08'	81° 15'	4
6. Kemgrovo, RSFSR, USSR	54° 00'	85° 20'	bulk seedlot.
7. Novosibirsk, RSFSR, USSR	55° 05'	82° 45'	bulk seedlot. *
8. Irkutsk, RSFSR, USSR	52° 15'	84° 20'	bulk seedlot.

* Same as population number 4, except that it does not have family structure.

In later chapters the populations will be designate as population 1 through 8 as shown in Table 1. Individual seedlot accession numbers are presented in Appendix 1.

Since no geographic and climatic information on seed origin locations was available from Canadian Forest Service, I have attempted to describe the seed source area based on information obtained from the literature. According to the latitudes, longitudes, and names of populations presented in Table 1, the area of seed origin lies within the West Siberian Lowland (Figure 1). This region is characterized by very low elevation and almost flat terrain that rarely exceeds 150 feet (46m) above sea level (Nuttonson 1950). From the publication titled *Agricultural Climatology of Siberia, Natural Belts and Agro-climatic Analogues in*

North America, by Nuttonson (1950), the following information can be drawn about the climate of the seed origins:

In the Novosibirsk oblast ('oblast' stands for province), two weather stations with approximately the same latitudes and longitudes as those of the seed sources provide the following information: The N. Nikolaevsk weather station (55° 00' N, 82° 33' E, 114m a.s.l.) shows that January (coldest month of the year) has an average temperature of -2.2°F (-19°C), whereas July (warmest month) has an average temperature of 65.5°F (18.6°C). The annual rainfall at the weather station is 15 inches (384.6mm), 71% of it falling between May and October and the rest is distributed almost evenly in the months between November and April, most likely as snow. The Novosibirsk weather station (54° 58' N, 82° 56' E, 133m a. s.l.) gives similar conditions. Here, the average temperatures of January and July are -2.7°F (-19°C) and 65.7°F (19°C), respectively. The annual rainfall at this station is 14.8 inches (379.5mm), 70% of it falling between May and October and the rest between November and April. These climatic conditions can be taken as approximate conditions for the 3 Novosibirsk, RSFSR, USSR populations in this study.

In the Kemerov oblast, conditions at the two weather stations give approximate conditions for the Kemgrovo, RSFSR, USSR populations in this study as follows: At Salair weather station (54° 17' N, 85° 49' E, 378m a.s.l.), the average temperature of the coldest month (January) is -0.3°F (-17.6°C) and the warmest month (July) is 66°F (19°C). The annual rainfall is 19.4 inches (497.4mm), 67% of it falling between May and September and 30% between November and February. The Stalinsk (Kuznetsk) weather station (53° 46' N, 87° 11' E, 207m a.s.l.) shows similar conditions where the average temperature of January and July is 0.9°F (-17°C) and 66.2°F (19°C), respectively. The annual rainfall is 19.3 inches

(494.9mm), 64% of it falling between May and September and 25% between October and January.

The Irkutsk, RSFSR, USSR population does not seem to come from the Irkutsk oblast. This is because the province is far removed from the probable seed source area in terms of longitudes. Thus, climatic conditions at the Irkutsk weather station as documented by Nuttonson (1950) cannot be taken to represent the conditions for the Irkutsk population in this study. The most likely origin of Irkutsk, RSFSR, USSR population is Itkulski Zavod in the Altai Kray. The climatic conditions at the Itkulski Zavod weather station (52° 41' N, 84° 37' E, 192m. a.s.l.) are, an average January temperature of 1.2°F (-17°C) and an average July temperature of 65.5°F (18.6 C). The annual rainfall is 21.9 inches (561.5mm), 78% of it falling between April and November.

2.2.2 Local Pine Seedlots

Since Scots pine is an exotic species in Alberta, two local pine populations, i.e., lodgepole pine and jack-lodgepole pine hybrid were included in the experiment as local controls. Their identities also appear in Appendix 1. Since comparison of Scots pine and local Canadian pines is out of the scope of this thesis, these local pine seedlots will not be discussed further.

2.3 Test Sites Description

The experiment was replicated on three test sites, namely Whitecourt Mountain Genetics Experimental Area (site A), Pine Ridge Forest Nursery (site B), and Swartz Creek Genetics Experimental Area (site C) (Table 2; Figure 2).

Table 2: Description of the three test sites used in Scots pine provenance - progeny tests in Alberta.

SITE	LAT. (N)	LONG. (W)	ELEV. (m.a.s.l)	TEMPERATURE (mean annual)		RAINFALL (mean monthly) (mm)	SOIL TYPE
				JAN. (°C).	JUL. (°C).		
A	54° 03'	115° 47'	823	-16.60	15.10	552.50	fertile, loam to silt-loam
B	54° 04'	112° 12'	610	-19.50	15.40	487.20	sandy
C	53° 23'	116° 30'	990	-14.40	15.00	572.00	sandy loam

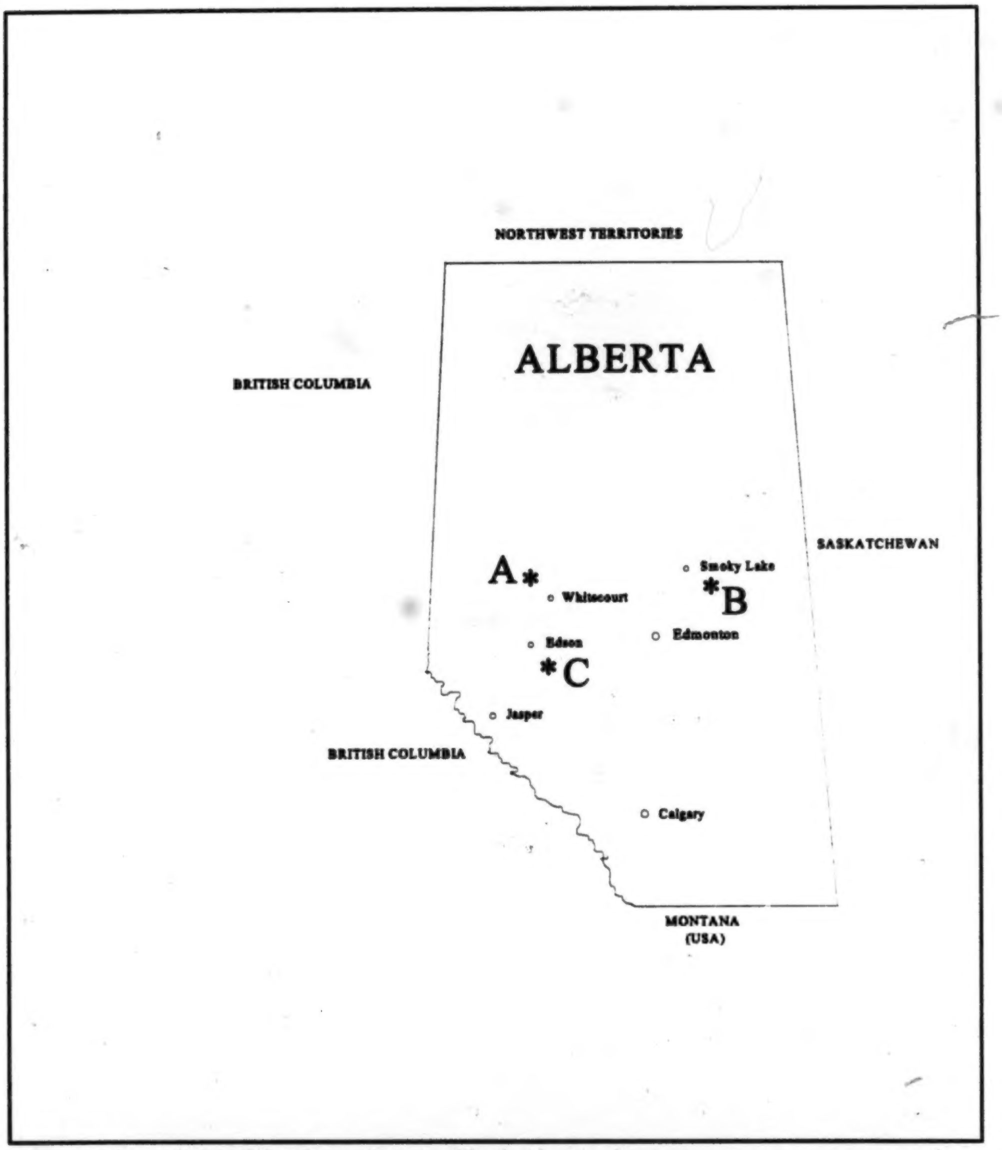

Figure 2: Locations of the three sites used in the Scots pine provenance - progeny study in Alberta. The asterisks show the approximate locations of the sites, whereas A, B and C refers to the test sites.

2.4 Raising of Planting Stock

Seeds were cold stratified for four weeks in January 1990 and sown into Spencer-Lemaire Tinus (350cc) containers, using a 3:1 peat to vermiculite potting mixture. Seedlings were grown in the greenhouse at Pine Ridge Tree Improvement Centre, using 18-hour photoperiod and approximately 25°/18°C day/night temperatures. Seedlings were hardened in June 1990 and moved to a shade frame, and later to heel-in beds for overwintering.

2.5 Field Planting and Experimental Design.

Field planting was done on 28 - 31 May 1991 at site B; 18 July 1991 at site C, and 26 - 27 July 1991 at site A. A randomized complete block experimental design with five replications and five-tree row plots was used at all three sites. Spacing between trees was 2.5 x 2.5m at site A and C, and 3 x 3m at site B. Notice that wider spacing was used at site B to facilitate mechanical weed control using a grass mower mounted on a tractor. Spacing differences between site B and the other two sites does not have any effect on tree growth differences at this time, since trees are still far apart. Because of seedling shortages, family 2914 was planted only at site A, and seedlots number 2897 and 2928 were short of one seedling in replication five at site B.

2.6. Field Tending

Site B received intensive management that was not provided at the other two sites. Because of its dry climate and sandy soils, trees were watered in the first two years of field establishment to ensure adequate survival, and fertilized in the third growing season. There was very good control of competing vegetation at site B, because of periodic mowing around the trees. There was neither irrigation nor fertilization of trees at sites A and C, and weed control at the two sites was less stringent. Weed control at these two sites consisted of manual weeding at irregular interval.

2.7. Field Measurements

Field measurements were done in the period between 19 September and 5 October 1995, i.e., 6 years from seed and completion of 5 years of field growth. At this time, shoot growth had completely ceased, and all trees had mature dormant buds on terminal and branch shoots, at all sites. At sites A and C, nearly all Scots pine trees had light-yellow to deep yellow needles.

(i) Height

All 5 trees in every plot were assessed for height at age 4 (H4), age 5 (H5) and age 6 (H6). Measurements were taken in centimetres (cm) as follows:

H6 = total tree height from the soil surface to the terminal bud,

H5 = tree height from the soil surface to the 1st whorl from the top,

H4 = tree height from the soil surface to the 2nd whorl from the top.

Notice that except where Lammas or other forms of secondary shoot growth are formed, Scots pine produces one whorl per year.

(ii) Branch Length

For every tree in the plot, lengths of the three longest branches in the 2nd whorl were measured. The length of a branch was measured in centimetres (cm) from the base of the branch (its attachment to the main tree stem) to the tip of the leading shoot of the branch. The average length of the three branches (MBL) was used for analysis.

(iii) Diameter

The diameters were measured in centimetres (cm) using the vernier caliper at the middle of the 1st internode (diameter 1 or D1) and at the middle of the 2nd internode (diameter 2 or D2).

(iv) Needle Length

Three needle fascicles from the eastern side of the 2nd whorl of every tree in the plot were randomly plucked, and the longest needle in each fascicle measured. Needles were measured in millimetres (mm) from the base to the tip. The average length of the three needles per tree, (MNL) was used in the analysis.

(v) Derived Traits

These are traits derived from height measurements as follows:

Height increment 1 (INC1) = H5 minus H4,

Height increment 2 (INC2) = H6 minus H5,

Average height increment (AINC) = {INC1 + INC2}/2,

Height growth from age 4 to age 6 here called total increment (TINC) = H6 minus H4.

2.8 Data Analyses

2.8.1 Analyses with Bulk Populations

The objective of analyzing the data without a family structure was to incorporate the three bulk populations into the analyses. This provided a framework for studying genetic variation at a population level using all eight or seven populations. This was done by ignoring family structure in populations where it existed. As already mentioned, population 4 and 7 came from the same seed source but were planted separately. Data were analyzed with the two populations separated and when they were pooled.

2.8.1.1 Single Site Analysis

Data were checked for conformity to normality and homogeneity of variances, which are important assumptions for the analysis of variances (Steel and Torrie 1980). The normality test was done, using the Lilliefors test and Shapiro- Wilks's test described in SPSS Inc. (1993). Both tests showed no significant ($P > 0.05$) departures from the normality assumption. The homogeneity of variances assumption was tested using the Levene test also described in SPSS Inc. (1993). There were no significant ($P > 0.05$) departures from the homogeneity of variances assumption. The data were, therefore, analyzed on an individual site basis without transformation. PROC VARCOMP with method type I (SAS Institute Inc. 1994) was used to generate the variance components. Hypotheses testing was done by the Satterthwaite (1946) method using the GLM 32 statistical software (Ye and Yeh 1996) because of missing cells at sites B and C. The following statistical model was employed on individual sites:

$$Y_{ijn} = \mu + R_i + P_j + RP_{ij} + E_{ijn}, \qquad (1)$$

where:

Y_{ijn} = observation on n-th tree in the j-th population planted in the i-th replication;

μ = site mean (fixed effect);

R_i = effect due to i-th replication, NID $(0, \sigma^2_r)$, i = 1,...,5;

P_j = effect due to j-th population, NID $(0, \sigma^2_p)$, j = 1,..., 8 or 7;

RP_{ij} = effect due to replication by population interaction, NID $(0, \sigma^2_{rp})$,

E_{ijn} = error associated with an observation on the n-th tree in the j-th population planted in the i-th replication, NID $(0, \sigma^2_e)$, n = 1,..., 5.

Except the mean (μ) all effects on the right-hand side of the model were considered random, independent, and normally distributed with zero mean and respective variances as indicated in the brackets. The ANOVA for this model is presented in Table 3.

Table 3: The ANOVA for the single site model without family structure.

SOURCE	DF	MS	EMS
Rep.	r - 1	MSR	$\sigma^2_e + k_1\sigma^2_{rp} + k_2\sigma^2_p + k_3\sigma^2_r$
Pop.	p - 1	MSP	$\sigma^2_e + k_4\sigma^2_{rp} + k_5\sigma^2_p$
Rep. x Pop.	(r-1)(p-1)	MSRP	$\sigma^2_e + k_6\sigma^2_{rp}$
Error	subtraction*	MSE	σ^2_e
Total	rpn - 1		

*Because of missing observations, the degrees of freedom for the error term are less than rp(n-1).

The percentage contribution to the total variance of each effect in the model was computed as follows:

$$\%(\sigma^2_x) = \frac{\sigma^2_x}{\sigma^2_y} \times 100, \qquad (2)$$

where:

σ^2_x = component of the variance attributable to the source of variation for which contribution is sought,

$\sigma^2_y = \sigma^2_e + \sigma^2_{rp} + \sigma^2_p + \sigma^2_r$ = total variance.

Negative variances were assumed to be zero (SAS Institute Inc. 1994). Therefore, all effects with negative variance components accounted for 0% of the total variance.

2.8.1.2 Across Site Analysis

Individual site data were merged with the exclusion seedlot 2914, which was not common to all three sites. The data were then checked for conformity to the normality and homogeneity of variances assumptions as described in section 2.8.1.1. There were no significant departures from the assumptions. Data were, therefore, analyzed without transformation as described in section 2.8.1.1, using the following statistical model:

$$Y_{dijn} = \mu + S_d + R_{i(d)} + P_j + SP_{dj} + RP_{ij(d)} + E_{dijn}, \qquad (3)$$

where:

Y_{dijn} = observation on n-th tree in the j-th population in the i-th replication within d-th test site;

S_d = effect due to d-th test site, NID (0, σ^2_s), d = 1,..,3;

$R_{i(d)}$ = effect due to i-th replication within d-th test site, NID (0, $\sigma^2_{r(s)}$), i = 1,...,5;

P_j = effect due to j-th population, NID (0, σ^2_p), j = 1,..., 8 or 7;

SP_{dj} = effect due to site x population interaction, NID $(0, \sigma^2_{sp})$;

$RP_{ij(d)}$ = effect due to replication by population interaction within d-th test site NID $(0, \sigma^2_{r(s)p})$;

E_{dijn} = error associated with an observation on the n-th tree in the j-th population in the i-th replication within d-th test site, NID $(0, \sigma^2_e)$, n = 1,...,5.

Other effects in the model are as defined in model 1. The ANOVA for this model is presented in Table 4.

Table 4: The ANOVA for the combine site model without family structure.

SOURCE	DF	MS	EMS
Site	s-1	MSS	$\sigma^2_e + k_1\sigma^2_{r(s)p} + k_2\sigma^2_{sp} + k_3\sigma^2_p + k_4\sigma^2_{r(s)} + k_5\sigma^2_s$
Rep (Site)	s(r-1)	MSR(S)	$\sigma^2_e + k_6\sigma^2_{r(s)p} + k_7\sigma^2_{sp} + k_8\sigma^2_p + k_9\sigma^2_{r(s)}$
Pop.	p-1	MSP	$\sigma^2_e + k_{10}\sigma^2_{r(s)p} + k_{11}\sigma^2_{sp} + k_{12}\sigma^2_p$
Site x Pop.	(s-1)(p-1)	MSSP	$\sigma^2_e + k_{13}\sigma^2_{r(s)p} + k_{14}\sigma^2_{sp}$
Rep (Site) x Pop.	s(r-1)(p-1)	MSRP(S)	$\sigma^2_e + k_{15}\sigma^2_{r(s)p}$
Error	subtraction*	MSE	σ^2_e
Total	srpn - 1		

* due to missing observations, the degrees of freedom the error term are less than srp(n-1)

The percentage contribution to the total variance of the effects in the model was computed according to equation 2, with:

$$\sigma^2_y = \sigma^2_e + \sigma^2_{rp(s)} + \sigma^2_{sp} + \sigma^2_p + \sigma^2_{r(s)} + \sigma^2_s$$

2.8.2 Analyses with Family Structure

The objective of analyzing the data with a family structure was to study genetic variation at a family-within-population level, and estimating genetic parameters needed to develop a breeding strategy for Scots pine. In these analyses, only five populations with a family structure were used (Table 1). To avoid confounding the population and family-within-population effects, the population effect was included in the statistical models. This was necessary, since preliminary analyses especally at site B showed that additive genetic variances could change, when the population effect was removed in the model.

2.8.2.1 Single Site Analysis

Data were checked for conformity to the normality and homogeneity of variances assumptions as described in section 2.8.1.1. There were no significant departures from the assumptions. Data were, therefore, analyzed on individual site basis without transformation as described in section 2.8.1.1, using the following statistical model:

$$Y_{ijkn} = \mu + R_i + P_j + RP_{ij} + F_{k(j)} + RF_{ik(j)} + E_{ijkn}\,, \qquad (4)$$

where:

Y_{ijkn} = observation on n-th tree in k-th family within j-th population planted in i-th replication,

μ = general mean (fixed effect),

R_i = effect due to i-th replication, NID $(0, \sigma^2_r)$, i = 1,...,5;

P_j = effect due to j-th population, NID $(0, \sigma^2_p)$, j = 1,...,5;

RP_{ij} = effect due to replication by population interaction, NID $(0, \sigma^2_{rp})$;

$F_{k(j)}$ = effect due to k-th family within j-th population, NID $(0, \sigma^2_{f(p)})$, k = 1, ...,29 or 30; *

$RF_{ik(j)}$ = effect due to replication by family interaction, NID (0, $\sigma^2_{rf(p)}$);

E_{ijkn} = within plot term, an error associated with an observation on the n-th tree in k-th family within j-th population planted in i-th replication, NID (0, σ^2_w), n = 1, ...,5.

* Since family 2914 was tested only at site A, k = 1,...,30 for site A and k = 1,...,29 for sites B and C. The ANOVA for this model is presented in Table 5.

Table 5: The ANOVA for the single site model with family structure.

SOURCE	DF	MS	EMS
Rep.	r-1	MSR	$\sigma^2_w + k_1\sigma^2_{rf(p)} + k_2\sigma^2_{f(p)} + k_3\sigma^2_{rp} + k_4\sigma^2_p + k_5\sigma^2_r$
Pop.	p-1	MSP	$\sigma^2_w + k_6\sigma^2_{rf(p)} + k_7\sigma^2_{f(p)} + k_8\sigma^2_{rp} + k_9\sigma^2_p$
Rep. x Pop.	(r-1)(p-1)	MSRP	$\sigma^2_w + k_{10}\sigma^2_{rf(p)} + k_{11}\sigma^2_{f(p)} + k_{12}\sigma^2_{rp}$
Fam (Pop.)	f-p-1	MSF(P)	$\sigma^2_w + k_{13}\sigma^2_{rf(p)} + k_{14}\sigma^2_{f(p)}$
Rep. x Fam(Pop.)	(r-1)(f-p)	MSRF(P)	$\sigma^2_w + k_{15}\sigma^2_{rf(p)}$
Error	subtraction	MSE	σ^2_w
Total	rpfn-1		

The percentage contribution to the total variance of the effects in the model was computed according to equation 2, with:

$$\sigma^2_y = \sigma^2_w + \sigma^2_{rf(p)} + \sigma^2_{f(p)} + \sigma^2_{rp} + \sigma^2_p + \sigma^2_r$$

2.8.2.2 Analysis Across Test Sites

The data for the three test sites were merged with the exclusion of family 2914, which was not common to all three sites. Data were then checked for conformity to the normality and homogeneity of variances assumptions as described in section 2.8.1.1 There were no significant departures from the assumptions. Data were, therefore, analyzed without transformation as described in section 2.8.1.1, using the following statistical model:

$$Y_{dijkn} = \mu + S_d + R_{i(d)} + P_j + SP_{dj} + RP_{ij(d)} + F_{k(j)} + SF_{dk(j)} + R_{i(d)}F_{k(j)} + E_{dijkn}, \qquad (5)$$

where:

Y_{dijkn} = observation on n-th tree in k-th family within j-th population planted in i-th replication within d-th test site;

$SF_{dk(j)}$ = effect due to site by family-within-population interaction, NID (0, $\sigma^2_{sf(p)}$);

$R_{i(d)}F_{k(j)}$ = residual term, an effect due to replication-within-site by family-within-population interaction, NID (0, σ^2_e);

E_{dijkn} = within plot term, an error associated with an observation on n-th tree in k-th family within j-th population planted in i-th replication within d-th test site, NID (0, σ^2_w), $n = 1,...,5$.

All other effects in the model are as previously defined. The ANOVA for this model is presented in Table 6.

Table 6: The ANOVA for the combined site model with family structure.

SOURCE	DF	MS	EMS
Site	s-1	MSS	$\sigma^2_w + k_1\sigma^2_e + k_2\sigma^2_{sf(p)} + k_3\sigma^2_{f(p)} + k_4\sigma^2_{r(s)p} + k_5\sigma^2_{sp} + k_6\sigma^2_p + k_7\sigma^2_{r(s)} + k_8\sigma^2_s$
Rep (Site)	s(r-1)	MSR(S)	$\sigma^2_w + k_9\sigma^2_e + k_{10}\sigma^2_{sf(p)} + k_{11}\sigma^2_{f(p)} + k_{12}\sigma^2_{r(s)p} + k_{13}\sigma^2_{sp} + k_{14}\sigma^2_p + k_{15}\sigma^2_{r(s)}$
Pop.	p-1	MSP	$\sigma^2_w + k_{16}\sigma^2_e + k_{17}\sigma^2_{sf(p)} + k_{18}\sigma^2_{f(p)} + k_{19}\sigma^2_{r(s)p} + k_{20}\sigma^2_{sp} + k_{21}\sigma^2_p$
Site x Pop.	(s-1)(p-1)	MSSP	$\sigma^2_w + k_{22}\sigma^2_e + k_{23}\sigma^2_{sf(p)} + k_{24}\sigma^2_{f(p)} + k_{25}\sigma^2_{r(s)p} + k_{26}\sigma^2_{sp}$
Rep (Site) x Pop.	s(r-1)(p-1)	MSRP(S)	$\sigma^2_w + k_{27}\sigma^2_e + k_{28}\sigma^2_{sf(p)} + k_{29}\sigma^2_{f(p)} + k_{30}\sigma^2_{r(s)p}$
Fam (Pop.)	f-p-1	MSF(P)	$\sigma^2_w + k_{31}\sigma^2_e + k_{32}\sigma^2_{sf(p)} + k_{33}\sigma^2_{f(p)}$
Site x Fam (Pop.)	(s-1)(f-p-1)	MSSF(P)	$\sigma^2_w + k_{34}\sigma^2_e + k_{35}\sigma^2_{sf(p)}$
Residual	s(r-1)(f-p)	MSE	$\sigma^2_w + k_{36}\sigma^2_e$
Within plot	subtraction	MSW	σ^2_w
Total	srpfn-1		

The percentage contribution to the total variance of the effect in the model was computed according to equation 2, with:

$$\sigma^2_y = \sigma^2_w + \sigma^2_e + \sigma^2_{sf(p)} + \sigma^2_{f(p)} + \sigma^2_{r(s)p} + \sigma^2_{sp} + \sigma^2_p + \sigma^2_{r(s)} + \sigma^2_s$$

2.8.2.3 Standard Errors of Variance Components

The standard errors of variance components for both individual and combined sites were estimated using the general formula given on page 33 in Becker (1975) as follows:

$$\sigma(\sigma^2_g) = \sqrt{\frac{2}{k^2}\sum\frac{MS_g^2}{f_g+2}} \quad , \qquad (6)$$

where:

k = coefficient of the variance component whose, standard error is being estimated,

MS_g = is the g-th mean square used to estimate the variance component,

f_g = degrees of freedom of the g-th mean square.

It is important at this point to mention that analysis of variances described in previous sections, both with bulk populations and with a family structure, were applied on quantitative variables only. Survival as a trait, was not analyzed by analysis of variances, since data recorded as alive (1) or dead (0) would seriously depart from normality and homogeneity of variances assumptions, even when transformed. Instead, the *One-Sample Chi-Square Test*, described on page 384 in SPSS Inc. (1993), was used to provide a simple measure of the significance of the differences in survival among populations, and families. This statistic has the following form:

$$\chi^2=\sum\frac{(O_i-E_i)^2}{E_i} \quad , \tag{7}$$

where:

O_i and E_i, equals observed and expected survivals, respectively.

For both populations and families, observed survival is the number of live trees in a population or family at the time of field assessment. Notice that populations were not equally represented in the test. Therefore, the population's expected survival, is the number of trees (percentage of total survival in the experiment), expected to fall in the population as reflected by its percentage representation in the experiment. Since families had equal representation in the experiment, their expected survival is the same, and equals average survival. The null hypothesis tested with this statistic was "all populations have equal survival rates." An alternative (research) hypothesis is "at least one population differs in survival rate from the rest." The same hypotheses apply for families.

2.8.2.4 Estimation of Heritability

2.8.2.4.1 The Heritability Concept

Narrow sense heritability is the ratio of the additive genetic variance to the phenotypic variance. It expresses the degree of correspondence between the breeding value and the phenotypic value of a quantitative trait (Falconer 1960). In other words, heritability is an indicator of the proportion of phenotypic variation that is due to additive genetic control. Symbolically, narrow sense heritability is expressed as:

$$h^2=\frac{V_A}{V_P} \quad , \tag{8}$$

where:

h^2 = narrow sense heritability, ranging from 0.0 to 1.0,

V_A= additive genetic variance, which is the portion of the genetic variance attributable to average effects of genes,

V_P = phenotypic variance, which is the sum of the genetic variance, environmental variance, and genotype by environment interaction variance, generally expressed as:

$$V_P = V_G + V_E + V_{GE} \quad , \tag{9}$$

where V_G, V_E, and V_{GE} stands for genetic variance, environmental variance and genotype by environment interaction variance, respectively.

By breaking the genetic component into additive and non-additive components, equation 9 becomes,

$$V_P = V_A + V_{NA} + V_E + V_{GE} \quad , \tag{10}$$

where V_{NA} = non-additive genetic variance. It is the sum of dominance and epistatic interaction variances (Mayo 1980).

Of these components of the phenotypic variance, the additive genetic variance V_A, which is the variance of breeding values, is the most important. This is because it is the component that determines the observable genetic properties of the population and its response to artificial selection (Falconer 1960). It follows from this fact that the ratio V_A/V_P, or simply heritability is the most important genetic parameter that influences breeding decisions (Falconer 1960).

Since genotypes can respond differently in different environments, heritabilities estimated with the same test material will vary from one place to another. Also, genotype responses may differ from time to time in response to time to time variation in environment. This may cause heritabilities to vary with time. It should also be understood that heritability is influenced by gene frequencies, and gene frequencies differ from one population to another (Falconer 1960). Therefore, heritability of a given trait, is a property of the population, environment, and time (Falconer 1960).

2.8.2.4.2 Single Site Heritability Estimation

Using the heritability concept outlined above, the single-site family and individual tree heritabilities for different traits were estimated using the formulae described on page 243 in Wright (1976) as follows:

$$h_i^2 = \frac{4\sigma^2_{f(p)}}{\sigma^2_w + \sigma^2_{rf(p)} + \sigma^2_{f(p)}} \quad , \qquad (11)$$

where:

h_i^2 = individual tree heritability,

$\sigma^2_{f(p)} = \frac{1}{4}V_A$ = 1/4 of additive genetic variance, since the variance component $\sigma^2_{f(p)}$ for half-sib families estimates only 1/4 of the additive genetic variance (Falconer 1960; Becker 1975; Wright 1976; Namkoong 1981).

$\sigma^2_w + \sigma^2_{rf(p)} + \sigma^2_{f(p)} = V_P$ = phenotypic variance.

Family heritabilities were computed as:

$$h_f^2 = \frac{\sigma^2_{f(p)}}{\frac{1}{k_{14}}\sigma^2_w + \frac{k_{13}}{k_{14}}\sigma^2_{rf(p)} + \sigma^2_{f(p)}} \quad , \qquad (12)$$

where:

h_f^2 = heritability for family means.

Other components in the formula are as previously defined.

2.8.2.4.3 Combined Sites Heritability Estimation

Individual tree and family heritabilities across test sites were computed as follows:

$$h_i^2 = \frac{4\sigma^2_{f(p)}}{\sigma^2_w + \sigma^2_e + \sigma^2_{sf(p)} + \sigma^2_{f(p)}} \quad , \qquad (13)$$

$$h_f^2 = \frac{\sigma^2_{f(p)}}{\frac{1}{k_{33}}\sigma^2_w + \frac{k_{31}}{k_{33}}\sigma^2_e + \frac{k_{32}}{k_{33}}\sigma^2_{sf(p)} + \sigma^2_{f(p)}} \quad , \qquad (14)$$

All items in the formulae are as previously defined.

2.8.2.4.4 Standard Errors of Heritability

Standard errors of individual tree heritabilities were computed using the formula given on page 38 in Becker (1975) as follows:

$$S.E(h_i^2) = 4\sqrt{\frac{2(n.-1)(1-t)^2[1+(k_1-1)t]^2}{k_1^2(n.-S)(S-1)}} \quad , \qquad (15)$$

where:

k_1 = coefficient of the family variance component,

n. = number of observations,

S = Number of families,

S - 1 = degrees of freedom for family source of variation,

t = interclass correlation.

Standard errors of family heritabilities were computed using the approximate formula given on page 244 in Wright (1976) as follows:

$$S.E(h_f^2)=\frac{(1-t)(1+kt)}{[k\frac{(F-1)}{2}]^{\frac{1}{2}}} \quad , \tag{16}$$

where:

k = coefficient of the family variance component,

F - 1 = degrees of freedom for family source of variation,

t = interclass correlation.

2.8.2.5 Estimation of Genetic and Phenotypic Correlations

2.8.2.5.1 Genetic and Phenotypic Correlations Between Traits

A correlation between two random variables is the ratio of their covariance to the product of their standard deviations (Steel and Torrie 1980). It is symbolically expressed as:

$$r_{XY}=\frac{Cov_{XY}}{\sqrt{\sigma_X^2\sigma_Y^2}} \quad , \tag{17}$$

where:

r_{XY} = correlation coefficient between variables X and Y,

Cov_{XY} = covariance of variables X and Y,

σ_X^2 and σ_Y^2 = variances of X and Y, respectively.

As in analysis of variances, the covariance can be partitioned into components attributable to different sources of variation (Kempthorne 1957; Falconer 1960). Correlations can then be computed with respect to every source of variation by substituting appropriate covariance and variance components in equation 17 (Kempthorne 1957).

As pointed out by Falconer (1960), the interest in studying correlations between traits in quantitative genetics lies in the need to understand the causes of correlation (either pleiotropy or linkage), the changes that selection on one trait can bring to other traits with which it is correlated, and the long-term effects of correlation between traits under natural selection. The first and third points are out of the scope of this thesis, but readers interested in the third point are referred to page 328 in Falconer (1960). Of all possible correlations, breeders are interested in the genetic correlation, i.e., the correlation of breeding values of two traits, because of its influence in breeding practices. In this study, the genetic correlations were computed after Falconer (1960) as:

$$r_{A_{XY}} = \frac{Cov_{A_{XY}}}{\sigma_{A_X}\sigma_{A_Y}} \quad , \qquad (18)$$

where:

$r_{A_{XY}}$ = additive genetic correlation between trait X and Y,

$Cov_{A_{XY}}$ = additive genetic covariance of traits X and Y,

σ_{A_X} and = σ_{A_Y} standard deviations of additive genetic variances for trait X and Y, respectively.

Similarly, the phenotypic correlations were computed as:

$$r_{P_{XY}} = \frac{Cov_{P_{XY}}}{\sigma_{P_X}\sigma_{P_Y}} \quad , \qquad (19)$$

where,

$r_{P_{XY}}$ = phenotypic correlation between traits X and Y,

$Cov_{P_{XY}}$ = phenotypic covariance of traits X and Y,

σ_{P_X} and σ_{P_Y} = standard deviations of phenotypic variances for trait X and Y, respectively.

2.8.2.5.2 Type B Genetic Correlations

Unlike a genetic correlation between traits, i.e., a correlation of two traits measured on the same individual, a Type B genetic correlation is a genetic correlation of the same trait measures on different individuals of the same family, reared in different environments (Hodge and White 1992). Therefore, a Type B genetic correlation is a measure of correspondence of family performances in different environments. The use of Type B genetic correlation is in studying the genotype by environment (G x E) interaction.

According to Yamada (1962) and Burdon (1977), a Type B genetic correlation has the following form:

$$r_{g_{XY}} = \frac{Cov_{g_{XY}}}{\sigma_{g_X}\sigma_{g_Y}} , \tag{20}$$

where:

$r_{g_{XY}}$ = genetic correlation of a trait as it is expressed at environment X and Y,

$Cov_{g_{XY}}$ = covariance for family means between the trait as it is expressed at environment X and Y,

σ_{g_X} and σ_{g_Y} = variances for family means at environment X and Y, respectively.

Notice that for half-sib families, the covariance and correlation refer to additive genetic covariance and correlation, i.e., $Cov_{g_{XY}} = \frac{1}{4} Cov_{A_{XY}}$ and $r_{g_{XY}} = r_{A_{XY}}$ (Burdon 1977).

In this study, Type B genetic correlations were computed as the ratio of the correlation between family means, and the products of the square roots of family heritability, as expressed at pairs of test sites. This method is described in formula 5 in Burdon (1977) as:

$$r_{A_{XY}} = \frac{r_{XY}}{h_{f_X} h_{f_Y}} , \tag{21}$$

where:

h_{f_X} and h_{f_Y} = square roots of family heritability for a trait at environment X and Y, respectively,

r_{XY} = correlation between family means at environment X and Y, and it is computed as:

$$r_{XY} = \frac{Cov_{A_{XY}}}{\sigma_{g_X} \sigma_{g_Y}} \quad , \tag{22}$$

where:

σ_{g_X} and σ_{g_Y} = square roots of the denominator used in computing family heritability at environment X and Y, respectively.

The standard errors of Type B genetic correlations were computed using the formula described on page 479 in Robertson (1959) as follows:

$$S.E(r_g) = \sqrt{\frac{[nt(1-r_g^2)+(1-t)]^2 + r_g^2(1-t)^2}{(N-1)n^2t^2} + \frac{r_g^2(1-t)^2}{N(n-1)n^2t_2}} \quad , \tag{23}$$

where:

r_g , t, $N - 1$, and n equal Type B genetic correlation, interclass correlation, degrees of freedom for the family-within-population effect, and number of trees per family, respectively.

The degree with which the Type B genetic correlation departs from unity, shows the importance of the G x E interaction in the test material. A correlation closer to one means minor or absence of the G x E interaction, whereas a correlation far below one means strong G x E interaction.

3. RESULTS

3.1 Geographic Variation

In this study, *geographic variation* implies genetic variation at a population level. In this context, populations are expected to differ genetically, primarily due to natural selection, because of habitat differences and the level of gene flow (migration) among them. If populations are small and isolated from each other, genetic drift may also cause population differentiation. Therefore, this section presents the results from the analysis of bulk populations. Since population 4 and 7 belong to the same seed source, this section gives emphasis on results in which the two populations are pooled. Results in which the two populations are separated appear in appendices only.

3.1.1 Height Growth

Except at age 4, where site C had higher average height than site B, the site means were in the order, site A > site B > site C (Table 7). At age 6, the average height at site A was 23.5% and 5.4% higher than the average height at sites C and B, respectively. The average height at site B was 17% higher than the average height at site C. At site A, the populations with the lowest mean heights ranged from 14.38% (H4) to 18.07% (H5) below the site means. The populations with the highest mean heights ranged from 2.44% (H6) to 4.35% (H4) above the site means. At site B, the populations with lowest mean heights ranged from 9.52% (H6) to 10.30% (H4) below the site means. The populations with the highest mean heights ranged from 6.27% (H6) to 9.04% (H4) above the site means. Deviations from the site means were much lower at site C. Here, the populations with the lowest mean heights ranged from 3.18% (H5) to 6.21% (H6) below the site means. Similarly, populations with the highest mean heights ranged from 2.7% (H5) to 3.95% (H4) above the site means.

Across test sites, the populations with the lowest mean heights were 9.84% (H4) and 11.14% (H6) below the general means. Populations with the highest mean heights ranged from 1.67% (H4) to 3.10% (H6) above the general means (Table 7).

Table 7: Range of population means for heights (cm), and their percentage deviations from the general mean, for bulk populations. Negative values denote below the mean.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	H4	66.39	80.91	77.54	-14.38	4.35	17.10
	H5	83.54	104.78	101.97	-18.07	2.76	17.58
	H6	126.46	155.11	151.41	-16.48	2.44	16.10
B	H4	54.09	65.75	60.30	-10.30	9.04	23.60
	H5	85.24	102.19	95.02	-10.29	7.55	20.62
	H6	129.93	152.61	143.61	-9.53	6.27	19.38
C	H4	69.00	74.65	71.81	-3.91	3.95	23.83
	H5	87.71	93.04	90.59	-3.18	2.70	21.74
	H6	115.00	127.38	122.62	-6.21	3.88	22.53
ACROSS	H4	62.94	70.98	69.81	-9.84	1.68	21.19
	H5	85.58	98.17	95.89	-10.75	2.38	19.76
	H6	124.01	143.88	139.55	-11.13	3.10	18.99

CV - coefficients of variation.

At site A, the percentage of the total variances attributable to the population effect was the lowest in H5 (2.05%) and the highest in H6 (2.64%) (Table 8). The percentage of the population variances decreased from 4.86% (H4) to 3.32% (H6) at site B. At site C, the population effect accounted for 0% of the total variance in H4 through H6.

Table 8: Variance components expressed as percentages of the total variance for height, with bulk populations at individual sites.

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	H4	1.03 NS	2.05 NS	6.25***	90.66
	H5	1.72 NS	2.47 NS	7.36***	88.45
	H6	2.61 NS	2.64 NS	6.90***	87.85
B	H4	0.21 NS	4.86**	1.29	93.65
	H5	0.84 NS	4.83**	1.77*	92.56
	H6	1.77 NS	3.32*	3.45*	91.46
C	H4	2.76*	0.00 NS	2.01	95.23
	H5	3.01*	0.00 NS	4.23	92.76
	H6	2.15 NS	0.00 NS	6.58**	91.27

* ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$)

Across sites, the population effect accounted for 0.01% of the total variance in H4, 0.56% in H5 and 1.02% in H6 (Table 9).

Table 9: Variance components expressed as percentages of the total variance for heights, with bulk populations across sites.

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
H4	23.95***	1.17 NS	0.01 NS	1.21*	2.39**	71.26
H5	6.05*	1.83*	0.56 NS	1.41*	4.25***	85.89
H6	20.56 ***	1.83*	1.02 NS	0.23 NS	4.52***	71.83

* ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$)

The within-population effect accounted for up to 90% of the total variance at site A, 93% at site B and 95% at site C. It accounted for between 71.26% and 85.89% cross sites. At sites A and C, the population by replication interaction accounted for greater percentage of the variances than the population effect (Table 8). At site B, the population by replication interaction was lower than the population effect. Except at H5, the site effect accounted for more than 20% of the total variance. The population by site interaction was the highest in H4 (1.21%) and the lowest in H6 (0.23%).

The population effect was statistically significant only at site B (Table 8). The population by replication interaction was significant in H4 through H6 at site A ($P < 0.001$), H4 and H5 at site B ($P < 0.05$) and H6 at site C ($P < 0.01$). Across sites, the population by site interaction was significant only in H4 and H5 ($P < 0.05$). The site effect was significant in H4 ($P < 0.001$), H5 ($P < 0.05$) and H6 ($P < 0.001$).

3.1.2 Height Increments

Generally, the height growth increments followed the order, site B > site A > site C (Table 10). The average height increment (AINC) at site B was 13% and 60% greater than AINC at sites A and C, respectively. The AINC at site A, was 42% greater than the corresponding value at site C. At site A, the means of the populations with the lowest and highest AINC were 14.22% and 4.50% below and above the site mean, respectively. The corresponding values were 9.74% and 4.78% at site B, and 4.99% and 3.55% at site C. When the three sites were analyzed jointly, the populations with the lowest and highest AINC were 9.81% and 4.75% below and above the mean, respectively.

Table 10: Range of population means for height increments (cm), and their percentage deviations from the general mean, for bulk populations. Negative values denote below the mean.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	INC1	19.87	25.97	24.85	-20.00	4.51	24.83
	INC2	42.92	51.71	49.39	-13.10	4.70	19.95
	AINC	31.93	38.86	37.20	-14.22	4.46	18.28
	TINC	63.87	77.71	74.36	-14.11	4.50	18.33
B	INC1	31.15	37.31	34.98	-10.95	6.66	24.49
	INC2	44.69	50.52	48.97	-8.74	3.16	21.68
	AINC	37.92	44.02	42.01	-9.74	4.78	19.81
	TINC	75.84	88.27	83.94	-9.65	5.16	20.06
C	INC1	18.39	19.72	19.05	-3.46	3.52	32.39
	INC2	30.15	34.56	33.29	-9.43	3.81	30.51
	AINC	24.92	27.16	26.23	-4.99	3.55	26.31
	TINC	49.84	54.32	52.46	-4.99	3.54	26.31
ACROSS	INC1	23.60	28.03	26.40	-10.61	6.17	26.73
	INC2	39.64	45.95	44.22	-10.34	3.91	23.14
	AINC	31.91	37.06	35.38	-9.81	4.75	20.85
	TINC	63.82	74.13	70.77	-9.82	4.75	20.89

CV - coefficients of variation.

The percentage of the variances for the population effect in AINC was greater at site A (2.31%) than at site B (1.91%) (Table 11). This is in contradiction with absolute heights in which the percentage of the variances was greater at site B than at site A. At site C, the population effect accounted for 0% of the total variance. At all three sites, the within-population effect accounted for approximately 90% of the total variance. The percentage of the variances for the population by replication interaction in height increments was, generally, greater than that of the population effect.

Table 11: Variance components expressed as percentages of the total variance for height increments, with bulk populations at individual sites.

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	INC1	5.11**	2.31*	2.02 NS	90.56
	INC2	2.86*	1.53 NS	3.39*	92.22
	AINC	5.10**	2.34*	2.52*	90.03
	TINC	5.12**	2.38*	2.57*	89.94
B	INC1	1.52 NS	3.11*	2.36**	93.01
	INC2	5.67**	0.53 NS	2.10*	91.69
	AINC	4.24*	1.91 NS	4.02**	89.82
	TINC	3.85*	2.00 NS	4.40**	89.75
C	INC1	2.51*	0.00 NS	3.03 NS	94.46
	INC2	0.03 NS	0.00 NS	7.18**	92.78
	AINC	1.24 NS	0.00 NS	7.80**	90.91
	TINC	1.24 NS	0.00 NS	7.80**	90.96

* ($P < 0.05$); ** ($P < 0.01$); NS = not significant ($P > 0.05$)

Across sites, the population effect accounted for 0.84% of the total variance in AINC. The sites effect, and the population by site interaction accounted for 50.57% and 0% of the total variance, respectively. The within-population effect accounted for 44.4% of the variance (Table 12).

Table 12: Variance components expressed as percentages of the total variance for heights, with bulk populations across sites.

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
INC1	54.06***	1.35**	0.72*	0.22 NS	1.09*	42.57
INC2	41.13***	1.80**	0.67**	0.00 NS	2.45***	53.95
AINC	50.57***	1.90**	0.84*	0.00 NS	2.28***	44.40
TINC	50.44***	1.88**	0.85*	0.00 NS	2.26 ***	44.58

* ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$)

The population effect for height increments was, statistically significant at site A (Table

11), but not at sites B and C. The population by replication interaction was significant at sites A ($P < 0.05$), and B and C ($P < 0.01$). Across sites, the population effect was statistically significant for all height increments due to lack of significant population by site interactions. The site effect was significant for all height increments ($P < 0.001$).

3.1.3 Diameter Growth

Diameter growth followed the order, site B > site A > site C (Table 13). For example, the mean diameters at the middle of the first internode (D1) were 3.96, 3.77 and 3.27cm for sites B, A and C, respectively.

Table 13: Range of population means for diameters (cm), and their percentage deviations from the general mean, for bulk populations. Negative values denote below the mean.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	D1	3.40	3.88	3.77	-9.81	2.92	20.79
	D2	2.82	3.20	3.13	-9.90	2.24	21.54
B	D1	3.56	4.21	3.96	-10.10	6.31	22.55
	D2	3.01	3.51	3.29	-8.51	6.69	23.45
C	D1	3.20	3.38	3.27	-2.14	3.36	20.79
	D2	2.57	2.72	2.64	-2.65	3.03	22.03
ACROSS	D1	3.41	3.80	3.68	-7.34	3.26	21.62
	D2	2.85	3.13	3.03	-5.94	3.30	22.58

CV - coefficients of variation.

At site A, populations with the lowest and highest mean diameters at the first internode (D1) were 9.81% and 2.92% below and above the site mean, respectively. The corresponding values were 10.1% and 6.31% at site B, and 2.14% and 3.36% at site C. Across sites, the means of the populations with the lowest and highest D1 were 7.34% and 3.26% below and above the general mean, respectively (Table 13).

At site B the population effect accounted for 1.93% of the total variance in D1 and 1.88% in D2. It accounted for 0% of the total variance in both D1 and D2 at sites A and C (Table 14). The percentage of the total variances attributable to the population by replication interaction was much greater than that of the population variance.

Table 14: Variance components expressed as percentages of the total variance for diameters, with bulk populations at individual sites.

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	D1	6.73**	0.00 NS	5.30**	87.97
	D2	6.24**	0.00 NS	4.68**	88.89
B	D1	7.18*	1.93 NS	5.57***	85.32
	D2	7.97**	1.88 NS	4.06**	86.09
C	D1	2.38*	0.00 NS	6.14**	91.48
	D2	4.38*	0.00 NS	8.51**	87.11

* ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$)

At all sites, the within-population effect accounted for more than 85% of the total variance in both D1 and D2. As for individual sites, the population effect accounted for approximately 0% of the total variance across sites (Table 15).

Table 15: Variance components expressed as percentages of the total variance for diameters, with bulk populations across sites.

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
D1	13.20**	5.45***	0.12 NS	0.24 NS	4.48***	76.51
D2	15.77**	5.68***	0.00 NS	0.31 NS	4.26***	73.97

** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$)

The population by site interaction accounted for 0.24% and 0.31% of the total variance in D1 and D2, respectively. Unlike absolute heights and height increments, the site effect was low. It accounted for 13.2% and 15.77% of the total variance in D1 and D2, respectively. The within-population effect accounted for 76.51% and 73.97% of the total variance in D1 and D2, respectively.

At all three sites and across sites, the population effect was not statistically significant in both D1 and D2. The population by replication interaction was, however, significant at all three sites ($P < 0.01$). Across sites, both the population effect and population by site interaction were not significant. However, the site effect was significant in both D1 and D2 ($P < 0.01$).

3.1.4 Branch and Needle Lengths

Branch and needle lengths followed the order, site B > site A > site C (Table 16). The mean branch length (MBL) for site B was 15% and 67% greater than those at sites A and C, respectively. At site A, the means of the populations with the lowest and highest MBL were 11.02% and 2.74% below and above the site mean, respectively. The corresponding values were 6.26% and 5.0% at site B, and 3.64% and 4.58% at site C. Across sites, the means of the populations with the lowest and highest MBL were 4.56% and 3.71% below and above the mean, respectively (Table 16).

Table 16: Range of population means for branch length (cm) and needle length (mm), and their percentage deviations from the general mean, for bulk populations. Negative values denote below the mean.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	MBL	35.76	41.29	40.19	-11.02	2.74	18.16
	MNL	49.59	57.52	55.67	-10.92	3.32	15.39
B	MBL	43.28	48.48	46.17	-6.26	5.00	22.27
	MNL	58.33	62.30	60.19	- 3.09	3.51	13.98
C	MBL	26.70	28.98	27.71	-3.64	4.58	27.26
	MNL	43.11	53.40	51.18	-15.77	4.34	18.26
ACROSS	MBL	36.80	39.99	38.56	-4.56	3.71	22.11
	MNL	50.31	57.98	55.98	-10.13	3.57	15.74

CV - coefficients of variation.

The average needle lengths (MNL) were 55.7, 60.19 and 51.2mm at sites A, B and C, respectively. At site A, the means of the populations with the lowest and highest MNL were 10.92% and 3.32% below and above the site mean, respectively. The corresponding values were 3.09% and 3.51% at site B, and 15.77% and 4.34% at site C. Across sites, the means of the populations with the lowest and highest MNL were 10.13% and 3.57% below and above the general mean, respectively (Table 16).

For MBL, the population effect accounted for 0.41%, 0.8% and 0% of the total variance at sites A, B and C, respectively (Table 17). The population by replication interaction accounted for 4.42%, 6.37% and 5.18% of the total variance at sites A, B and C, respectively. The within-population effect accounted for 90.08%, 87.63% and 93.23% of the total variance at sites A, B and C, respectively.

Table 17: Variance components expressed as percentages of the total variance for branch and needle lengths, with bulk populations across sites.

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	MBL	5.09**	0.41 NS	4.42*	90.08
	MNL	0.78 NS	1.73 NS	5.47***	92.01
B	MBL	5.19*	0.80 NS	6.37***	87.63
	MNL	7.89**	0.49 NS	1.46 NS	90.16
C	MBL	1.59 NS	0.00 NS	5.18**	93.23
	MNL	11.32***	3.43**	0.10 NS	85.15

* (P < 0.05); ** (P < 0.01); *** (P < 0.001); NS = not significant (P > 0.05)

For MNL, the population effect accounted for only 0.49% of the total variance at site B. It accounted for 1.73% and 3.43% of the total variance at sites A and C, respectively. The population by replication interaction accounted for 5.47%, 1.46% and 0.1% of the total variance at sites A, B and C, respectively. Similarly, the within-population effect accounted for 92.01%, 90.16% and 85.15% of the total variance at sites A, B, and C, respectively.

Across sites, the population effect and population by site interaction accounted for 0.2% and 0% of the total variance, respectively, in MBL (Table 18). The site and within-population effects accounted for 50.36% and 44.45% of the total variance, respectively, in MBL. For MNL, the population effect accounted for only 0.84% of the total variance. Respectively, the site effect, population by site interaction, and within-population effect accounted for 18.75%, 0% and 76.23% of the total variance in MNL (Table 18).

Table Variance: 18 components expressed as percentages of the total variance for branch and needle lengths, with bulk populations across sites.

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
MBL	50.36***	2.27***	0.20 NS	0.00 NS	2.72***	44.45
MNL	18.75**	1.90***	0.84**	0.00 NS	2.28**	76.23

** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$)

For MBL, the population effect was not statistically significant at all three sites and across sites. The population by replication interaction was, however, significant at sites A ($P < 0.05$), B ($P < 0.001$) and C ($P < 0.01$). While the site effect was significant ($P < 0.001$), the population by site interaction was not significant. For MNL, the population effect was significant only at site C (Table 17). It was also significant across sites due to the absence of a significant population by site interaction (Table 18). The population by replication interaction was significant only at site A ($P < 0.001$).

3.1.5 Population Survival

Generally, the rates of survival of populations followed the order, site A > site B > site C. Total survival rates were, 98.2% at site A, 92.9 at site B, 87.1% at site C, and 92.7% across sites. Rates of survival were generally high for all populations on all three test sites (Table 19). Although populations showed different percentage survivals at each site, the differences were statistically not significant ($P > 0.05$), based on Chi-Square described in section 2.8.1.2. Except population 6 that showed the highest percentage survival at sites A and C, but the lowest survival at site B (Table 19), rates of population survival were consistent across sites.

Table 19: Survival percentages and Chi-Square tests for Scots pine populations on individual and across test sites

POPULATION	SITE A	SITE B	SITE C	ACROSS
1	96.8	88.7	88.0	90.9
2	98.4	93.2	88.8	93.5
3	97.6	94.0	89.0	93.8
4	97.7	99.4	84.6	93.4
5	100.0	89.0	83.0	90.7
6	100.0	76.0	92.0	89.3
8	100.0	91.7	88.0	92.0
Mean	98.6	90.3	87.6	91.9
χ^2	0.13 NS	1.91 NS	0.56 NS	0.60 NS
DF	6	6	6	6

NS = not significant ($P > 0.05$)

3.2 Genetic Variation and Heritabilities

In this study, genetic variation refers to variation at a family-within-population level. Therefore, this section presents results from analyses of data with a family structure. Greater emphasis will be given to the family-within-population effect than other sources of variation. Details for other effects in the single-sites and across sites models appear appendices. Also, presented in this section are genetic parameters for different traits.

3.2.1 Height Growth

Except for H4 where the mean height on site C was higher than that on site B, height growth followed the order, site A > site B > site C (Table 20). At 6 years from seed (H6), the families with the lowest and highest mean heights were 15.59% and 14.88% below and above the site mean, respectively, at site A. The corresponding values were 14.67% and 12.61% at site B, and 9.13% and 13.66% at site C. More or less similar trend was observed in H4 and H5 at all sites. The range of family mean deviations from site means was the highest in H5 at site A. Across sites, the families with the lowest and highest mean heights at age 6 were 7.31% and 10.64% below and above the general mean, respectively. Family mean deviations with age was more consistent across sites than at individual sites.

Table 20: Range of family means for heights (cm), and their percentage deviations from the general mean. Negative values denote below the mean. Family 2914 was excluded across sites.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A[1]	H4	65.62	91.13	78.05	-15.93	16.76	15.33
	H5	87.04	122.62	102.90	-15.41	19.16	16.03
	H6	130.78	175.92	153.13	-15.59	14.88	14.00
B	H4	50.35	69.61	60.16	-16.31	15.71	21.47
	H5	81.30	110.10	95.03	-14.45	15.86	18.51
	H6	122.85	162.13	143.98	-14.68	12.61	17.28
C	H4	60.10	83.76	71.88	-16.39	16.53	21.55
	H5	77.91	103.33	91.19	-14.56	13.31	19.16
	H6	112.38	140.57	123.67	-9.13	13.66	19.87
ACROSS[1]	H4	65.74	78.43	69.81	-5.83	12.35	19.73
	H5	89.88	108.38	96.45	-6.81	12.37	18.25
	H6	130.03	155.20	140.28	-7.31	10.64	17.40

A[1] - family 2914 included; ACROSS[1] - A, B & C combined; CV - coefficients of variation.

The additive genetic variance (family-within-population) generally followed the order, site C > site A > site B (Table 21). At sites A and C, the standard errors of the additive genetic variances were approximately half the variances. At site B, however, the standard errors were greater than the variances, except in H4 where the error was a little greater than 50% of the variance.

Table 21: The additive genetic variances for heights on individual sites and across sites. Family 2914 was excluded across sites.

TRAIT	SITE A^1	SITE B	SITE C	ACROSS^1	ACROSS^2
H4	13.53 ± 6.78**	11.68 ± 6.92*	22.42 ± 11.81**	2.77 ± 3.68 NS	9.34 ± 6.51*
H5	25.84 ± 12.63**	9.87 ± 10.76 NS	32.00 ± 15.35**	9.12 ± 6.15 NS	14.81 ± 9.33*
H6	48.97 ± 23.06**	20.16 ± 21.48 NS	47.32 ± 25.86**	12.64 ± 11.48 NS	19.40 ± 17.61*

A^1 - family 2914 included; ACROSS^1 - A, B & C combined; ACROSS^2 -A & C combined; * ($P < 0.05$); ** ($P < 0.01$); NS = not significant ($P > 0.05$).

When the three sites were considered together, the additive genetic variance across sites was much lower than that observed at individual sites, except at age H5 where the variance across sites was comparable to that of site B. The standard error was greater than the variance in H4, 75% of the variance in H5, and approximately equal to the variance in H6. When site B was removed from analysis across sites, the additive genetic variance across sites increased (Table 21). However, except at age 4, the relative size between the variance components and their standard errors, remained almost the same as when site B was included. The variance components for all effects in single-site and across-sites models (when all three sites are involved) appear in Appendix 10 and 11, respectively.

At age 6, the additive genetic variance accounted for 7.36% of the total variance at site A, 2.5% at site B, and 6.03% at site C (Table 22). There was, however, a considerable reduction in the percentage of the variance at site A, when family 2914 was excluded from the analysis. The percentage of the variance at age 6 for site A is consistent with variances at age 4 and 5. There were only small changes in the percentage of the variance at site C. At site B, however, the percentages of the variance at age 5 and 6 were only half the percentage of the variance at age 4. Across sites, the additive genetic variance accounted for lower percentage of the total variances when all three sites were involved, than when only sites A and C were involved (Table 22).

Table 22: The additive genetic variances for heights expressed as percentages of the total variance on individual sites and across sites. Family 2914 was excluded across sites.

TRAIT	SITE A^1	SITE A^2	SITE B	SITE C	ACROSS^1	ACROSS^2
H4	7.04**	4.20*	5.59**	7.36**	0.88 NS	3.38*
H5	7.06**	3.33*	2.48 NS	8.04**	2.15 NS	3.33*
H6	7.36**	4.81*	2.50 NS	6.03**	1.32 NS	1.77*

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined: ACROSS^2 -A & C combined; * ($P < 0.05$); ** ($P < 0.01$); NS = not significant ($P > 0.05$).

At age 6, the family by replication interaction effect accounted for 10.97%, 15.21% and 8.56% of the total variance at sites A, B and C, respectively. The within-family effect accounted for 74.45% of the total variance at site A, 76.82% at site B, and 77% at site C. Appendices 12 and 13 present the percentages of the variance components for all effects in the single-site model. Across sites, the site effect, family by site interaction, and within-family effect accounted for 18.64%, 2.92% and 62.11% of the total variance, respectively at age 6, when all three sites were involved. Percentages of the variance components for all effects in the combined-sites model are presented in Appendix 14.

The family-within-population effect was statistically significant for H4 through H6, at sites A and C. It was significant only in H4 at site B. Across sites, the family-within-population effect was not significant when all three sites were jointly considered, for H4 through H6. It was, however, marginally significant when site B was removed from the analysis. The family by replication interaction was significant for H4 through H6 at sites A and B ($P < 0.001$), and site C ($P < 0.001$, $P < 0.01$, $P < 0.05$, respectively). When all three sites were considered jointly, the site effect was significant in H4 and H6 ($P < 0.001$) and H5 ($P < 0.05$). Similarly, the family by site interaction was significant in H4 ($P < 0.01$), and H5 and H6 ($P < 0.05$).

Heritability estimates were higher at sites A and C than at site B and across sites (Table 23). At age 6 for example, individual tree and family heritability estimates for site B were respectively one third and half the estimates at sites A and C. There were reductions in the heritability estimates at site A when family 2914 was excluded from the analysis.

Table 23: Heritability estimates and their standard errors for heights on individual sites and cross sites. Family 2914 was excluded across sites.

SITE	TRAIT	h_i^2	$S.E(h_i^2)$	h_f^2	$S.E(h_f^2)$
A^1	H4	0.30	0.10	0.56	0.15
	H5	0.30	0.12	0.57	0.15
	H6	0.34	0.13	0.59	0.16
A^2	H4	0.18	0.10	0.42	0.12
	H5	0.14	0.08	0.37	0.10
	H6	0.21	0.10	0.55	0.13
B	H4	0.23	0.11	0.48	0.13
	H5	0.10	0.08	0.27	0.09
	H6	0.11	0.08	0.23	0.09
C	H4	0.30	0.13	0.54	0.15
	H5	0.34	0.14	0.59	0.16
	H6	0.26	0.12	0.52	0.14
$ACROSS^1$	H4	0.05	0.03	0.24	0.06
	H5	0.10	0.04	0.45	0.09
	H6	0.07	0.04	0.34	0.07
$ACROSS^2$	H4	0.15	0.07	0.46	0.11
	H5	0.16	0.07	0.50	0.12
	H6	0.11	0.06	0.37	0.09

A^1 -family 2914 included; A^2 -family 2914 excluded; $ACROSS^1$ -A, B & C combined; $ACROSS^2$ -A & C combined.

The standard errors of heritabilities were less than 50% for both individual tree and family heritabilities at sites A and C. At site B, the standard errors of family heritabilities were one third of heritability estimates. The errors of individual tree heritabilities were 80% of heritability estimates for H5 and H6, and only 50% of the heritability for H4.

Across sites, individual tree heritability for H4 tripled with removal of site B from analysis, whereas family heritability for the same trait doubled (Table 23). There were also increases in individual and family heritability for H5 and H6 when site B was removed from analysis. Standard errors of individual tree heritabilities for H4 and H6 were a little greater than 50% of heritability estimates, when all three sites were involved, and in H6 when site B was excluded. For H4 and H5, standard errors of individual tree heritabilities were a little less than 50% of heritability estimates when site B was excluded. Standard errors of family heritabilities across sites were between one quarter and one fifth of heritability estimates no matter whether site B was in or out.

The pattern of heritabilities at site A when family 2914 is included in the analysis reflects a gradual increase in height heritability with age. However, this pattern disappears when family 2914 is excluded from the analysis. Both family and individual tree heritability estimates for site B, C and across sites does not reflect any pattern with age of trees.

3.2.2 Height Increments

Height increments followed the order, site B > site A > site C. The average increments (AINC) were 37.45cm at site A, 42.06cm at site B and 26.42cm at site C (Table 24). At site A, the means of families with the lowest and highest AINC were 14.39% and 15.03% below and above the site mean, respectively. The corresponding values were 14.5% and 9.98% at site B, and 17.98% and 17.83% below and above the mean at site C. Across sites, the means of families with the lowest and highest AINC were 11.01% and 12.94% below and above the mean, respectively.

Table 24: Range of family means for heights (cm), and their percentage deviations from the general mean. Negative values denote below the mean. Family 2914 was excluded across sites.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A[1]	INC1	21.21	29.96	24.99	-15.13	19.89	23.11
	INC2	42.83	57.40	49.79	-13.98	15.28	17.34
	AINC	32.06	43.08	37.45	-14.39	15.03	16.00
	TINC	64.13	86.16	74.90	-14.38	15.03	16.00
B	INC1	30.29	40.49	35.02	-13.51	15.62	23.26
	INC2	41.55	52.27	49.04	-15.27	6.59	19.58
	AINC	35.96	46.26	42.06	-14.50	9.98	18.07
	TINC	71.92	92.52	84.11	-14.49	10.00	18.18
C	INC1	13.48	21.95	19.14	-29.57	14.68	30.70
	INC2	26.31	40.50	33.67	-21.86	20.28	28.63
	AINC	21.67	31.13	26.42	-17.98	17.83	24.62
	TINC	43.33	62.26	52.74	-17.84	18.05	24.94
ACROSS[1]	INC1	23.34	29.88	26.55	-12.09	12.54	25.80
	INC2	39.37	50.09	44.43	-11.39	12.74	21.39
	AINC	31.56	40.06	35.52	-11.15	12.78	19.30
	TINC	63.12	80.11	70.93	-11.01	12.94	19.48

A[1] - family 2914 included; ACROSS[1] - A, B & C combined; CV - coefficients of variation.

The additive genetic variances for height increments were the highest at site A (Table 25). For example, the additive genetic variance for AINC at site B was 66% of the variance at site A. The corresponding variance at site C was only 49% of the variance at site A. The standard errors of the additive genetic variances ranged from 56% to 72% of the variance at site A. At site B, errors were greater than the variances, whereas at site C, they were between 58% and 85% of the variance. Across sites, the standard errors ranged from 61% to 77% of the variance when all three sites were involved. Only in INC1 did the standard error exceed the variance component across sites. Notice that, unlike absolute heights, removal of site B from analysis did not greatly change the amount of the additive genetic variance (Table 25).

Table 25: The additive genetic variances for heights on individual sites and across sites. Family 2914 was excluded across sites.

TRAIT	SITE A^1	SITE B	SITE C	ACROSS^1	ACROSS^2
INC1	1.61 ± 1.16*	1.74 ± 1.89 NS	1.30 ± 1.10 NS	0.20 ± 0.35*	0.11 ± 0.69 NS
INC2	6.00 ± 3.35*	3.07 ± 3.38 NS	5.68 ± 3.28 **	2.18 ± 1.69 NS	3.64 ± 2.61 NS
AINC	2.94 ± 1.67**	1.94 ± 2.11 NS	1.92 ± 1.43 *	1.45 ± 0.89*	1.31 ± 1.14 NS
TINC	11.75 ± 6.69**	7.29 ± 8.29 NS	8.17 ± 5.86*	5.81 ± 3.61*	5.21 ± 4.64 NS

A^1 -family 2914 included; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined; ** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$).

The pattern of the additive genetic variances for height increments was consistent with the pattern of the variance for absolute heights. For example, the additive genetic variances for both height and height increments at site B were associated with high standard errors, whereas the opposite was the case, at sites A and C. The variance components for all effects in the single-site and across-site models appear in Appendices 10 and 11, respectively.

The additive genetic variance was 5.92%, 2.51%, 3.59% of the total variance for AINC at sites A, B and C, respectively (Table 26). Without family 2914 at site A, the additive genetic variance dropped to 4.29% of the total variance for AINC. Across sites, the additive genetic variance accounted for 1.19% and 1.2% of the total variance for AINC when site B was included and when removed from the analysis, respectively.

Table 26: The additive genetic variances for heights expressed as percentages of the total variance on individual sites and across sites. Family 2914 was excluded across sites.

TRAIT	SITE A^1	SITE A^2	SITE B	SITE C	ACROSS^1	ACROSS^2
INC1	3.75*	0.86 NS	2.19 NS	3.10 NS	0.17*	0.18 NS
INC2	6.07*	5.65**	2.49 NS	5.04 **	1.14 NS	1.49 NS
AINC	5.92**	4.29*	2.51 NS	3.59*	1.19 *	1.20 NS
TINC	5.92**	4.30*	2.34 NS	3.77*	1.18*	1.18 NS

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined; ** ($P < 0.01$); *** ($P < 0.001$); NS = not significant ($P > 0.05$).

The family by replication interaction accounted for 14.86%, 16.33% and 7.98% of the total variance for AINC at sites A, B and C, respectively. Also for AINC, the within-family effect accounted for 72.37%, 74.76% and 79.06% of the total variance at sites A, B and C, respectively. Appendices 12 and 13 present the percentages of variance components for all effects in the single-site model. Across sites, the site effect, family by site interaction, and within-family effect, respectively accounted for 48.68%, 0.61% and 38.51% of the total variance for AINC. The percentages of variance components for all effects in the combined site model appear in Appendix 14.

Except INC1 at site C, the family-within-population effect was statistically significant for all height increments at sites A and C (Table 25). It was not significant at site B. The family by replication interaction was significant for all height increments at sites A and B ($P < 0.001$). It was only significant for INC1 at site C ($P < 0.001$). Hypotheses tests for all effects in the single-site model for height increments appear in Appendices 15 through 17. Across sites, the family-within-population effect was significant for all height increments except INC2 when all three sites were considered jointly. It was not significant for all increments when site B was excluded. The family by site interaction was not significant for height increments except INC2 when all three sites were involved. However, the site effect was highly significant (P < 0.001). Appendix 18 presents hypotheses tests for all effects in the combined-site model for all height increments when all three sites were involved.

Heritability estimates for height increments were the lowest at site B (Table 27). As for absolute heights, the ratio of the standard errors to the heritability estimates were higher at site B than at the other two sites and across sites. At site A, the exclusion of family 2914 from the analysis caused some reductions in heritability estimates. In INC1 for example, individual tree and family heritability without family 2914 were only 23% and 33% of heritabilities with family 2914. Notice that, while heritabilities of height increments across sites did not change greatly with removal of site B from analysis, heritability for INC1 was severely reduced (Table 27). Generally, heritability estimates for height increments were lower than estimates for absolute heights.

Table 27: Heritability estimates and their standard errors for heights on individual sites and cross sites. Family 2914 was excluded across sites.

SITE	TRAIT	h_i^2	$S.E(h_i^2)$	h_f^2	$S.E(h_f^2)$
A^1	INC1	0.16	0.09	0.40	0.11
	INC2	0.25	0.11	0.50	0.14
	AINC	0.25	0.11	0.49	0.14
	TINC	0.25	0.11	0.49	0.14
A^2	INC1	0.04	0.06	0.13	0.07
	INC2	0.24	0.11	0.49	0.13
	AINC	0.18	0.10	0.41	0.12
	TINC	0.19	0.10	0.41	0.12
B	INC1	0.09	0.08	0.27	0.09
	INC2	0.11	0.08	0.27	0.09
	AINC	0.11	0.08	0.27	0.09
	TINC	0.10	0.08	0.26	0.09
C	INC1	0.13	0.09	0.35	0.10
	INC2	0.22	0.11	0.50	0.13
	AINC	0.16	0.10	0.39	0.11
	TINC	0.16	0.10	0.40	0.11
ACROSS^1	INC1	0.07	0.04	0.47	0.08
	INC2	0.08	0.04	0.39	0.08
	AINC	0.10	0.04	0.49	0.09
	TINC	0.10	0.04	0.48	0.09
ACROSS^2	INC1	0.01	0.03	0.06	0.05
	INC2	0.13	0.06	0.43	0.10
	AINC	0.10	0.05	0.38	0.09
	TINC	0.10	0.05	0.37	0.09

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined.

3.2.3 Diameter Growth

Diameter growth across sites followed the order, site B > site A > site C. At 6 years from seeds, the diameters at the middle of the first internode (D1) were, 3.79cm, 3.96cm, and 3.26cm at site A, B and C, respectively (Table 28).

Table 28: Range of family means for diameters (cm), and their percentage deviations from the general mean. Negative values denote below the mean. Family 2914 was excluded across sites.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A^1	D1	3.39	4.15	3.79	-10.55	9.50	19.03
	D2	2.80	3.56	3.15	-11.11	13.02	19.69
B	D1	3.14	4.40	3.96	-20.71	11.11	19.27
	D2	2.64	3.71	3.28	-19.51	13.11	19.61
C	D1	2.50	3.66	3.26	-23.31	12.27	19.41
	D2	2.17	3.02	2.64	-17.80	14.39	19.84
ACROSS^1	D1	3.42	3.96	3.68	-7.06	7.61	19.58
	D2	2.85	3.29	3.03	-5.94	8.58	20.29

A^1 - family 2914 included; ACROSS^1 - A, B & C combined; CV - coefficients of variation.

At site A, the means of families with the lowest and highest D1 were 10.55% and 9.5% below and above the site mean, respectively. The corresponding values were 20.7% and 11.11% at site B, and 23.31% and 12.27% at site C. Across sites, the means of families with the lowest and highest D1 were 7.06% and 7.61% above and below the mean, respectively.

As in height and height increments, the standard errors of the additive genetic variances at site B were greater than the variance estimates (Table 29). The standard errors were lower than the variance estimates at sites A and C. Across sites, the variances were zero (negative) for both D1 and D2 when the three sites were involved in the analysis. When site B was excluded from analysis, the additive genetic variances and the standard errors were equal, i.e., 0.01. The variance components for all effects in the single and combined sites models appear in Appendices 10 and 11, respectively.

Table 29: The additive genetic variances (above), and the additive genetic variances as percentages of the total variance (below) for diameters on individual sites and across sites. Family 2914 was excluded across sites.

TRAIT	SITE A^1	SITE B	SITE C	ACROSS^1	ACROSS^2
D1	0.021±0.017 NS	0.0048±0.024 NS	0.025±0.017 NS	0.00 NS	0.01 ± 0.01 NS
D2	0.012±0.011 NS	0.0102±0.021 NS	0.017±0.013 NS	0.00 NS	0.01 ± 0.01 *
D1	3.03	0.51	4.61	0.00	1.25
D2	2.44	1.49	4.38	0.00	1.64
D1(A^2)	2.94*				
D2 (A^2)	2.01				

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined; * ($P < 0.05$).

For D1, the additive genetic variance was 3.03% of the total variance at site A, 0.51% at site B, and 4.61% at site C (Table 29). Of the total variance, the family by replication interaction accounted for 11.67% at site A, 28.54% at site B and 15.68% at site C. The within-family effect accounted for 74.93%, 61.32% and 73.79% of the total variance for D1 at sites A, B, and C, respectively. When site B was excluded from analysis, the additive genetic variance accounted for 1.25% of the total variance for D1.

The family-within-population effect was not statistically significant at all sites and across sites, except for D2 when site B was excluded from analysis. The family by replication interaction effect for both D1 and D2 was highly significant ($P < 0.001$) at all sites. Across sites, the site effect was significant ($P \leq 0.01$) for both D1 and D2. The family by site interaction was, however, not significant. Hypotheses tests for all effects in the single-site and combined-site models appear in Appendices 15 through 18.

As in other traits, heritability values were the lowest at site B (Table 30). The standard errors of heritabilities for site B were predominantly greater than heritability values. At both sites A and C, the standard errors were lower than heritability estimates. At sites A and C, heritability values declined with age, whereas heritability increased with age at site B. Generally, heritability values for diameters were lower than the corresponding values for heights.

Table 30: Heritability estimates and their standard errors for diameters on individual sites and cross sites. Family 2914 was excluded across sites.

SITE	TRAIT	h_i^2	$S.E(h_i^2)$	h_f^2	$S.E(h_f^2)$
A^1	D1	0.13	0.08	0.35	0.10
	D2	0.11	0.07	0.31	0.09
A^2	D1	0.13	0.08	0.35	0.10
	D2	0.09	0.07	0.27	0.09
B	D1	0.02	0.06	0.06	0.07
	D2	0.06	0.07	0.15	0.08
C	D1	0.20	0.11	0.40	0.12
	D2	0.19	0.11	0.39	0.12
ACROSS^1	D1	0.00	0.00	0.00	0.00
	D2	0.00	0.00	0.00	0.00
ACROSS^2	D1	0.07	0.04	0.33	0.08
	D2	0.09	0.05	0.33	0.08

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined.

3.2.4 Branch and Needle Lengths

The average branch lengths were in the order, site B > site A > site C (Table 31). At site A, the means of families with the lowest and highest average branch length (MBL) were 14.89% and 10.15% below and above the mean, respectively. The corresponding values were 12.77% and 11.34% at site B, 19.08% and 17.1% at site C , and 8.92% and 11.23% across sites. Needles were the longest at site B and the shortest at site C (Table 31). At site A, the means of families with the shortest and longest average needle length (MNL) were 13.53% and 8.54% below and above the mean, respectively. The corresponding values were 4.7% and 9.31% at site B, 8.69% and 15.22% at site C, and 8.07% and 10.21% across sites.

Table 31: Range of family means for branch length (cm), and needle length (mm) and their percentage deviations from the general mean. Negative values denote below the mean. Family 2914 was excluded across sites.

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A[1]	MBL	34.47	44.61	40.50	-14.89	10.15	16.02
	MNL	48.19	60.49	55.73	-13.53	8.54	13.18
B	MBL	40.76	52.03	46.73	-12.78	11.34	18.51
	MNL	57.84	66.34	60.69	-4.70	9.31	12.60
C	MBL	22.47	32.52	27.77	-19.08	17.10	25.64
	MNL	47.08	59.41	51.56	-8.69	15.22	17.56
ACROSS[1]	MBL	35.21	43.00	38.66	-8.92	11.22	20.96
	MNL	51.70	61.98	56.24	-8.07	10.21	14.82

A[1] - family 2914 included; ACROSS[1] - A, B & C combined; CV - coefficients of variation.

The additive genetic variance for MBL was negative at site B, but positive at sites A, C and across sites. Standard errors of the variances were low at site A and across sites. At site C, the error was approximately equal to the variance estimate (Table 32). For MNL, the additive genetic variance was the highest at site A, and the lowest at site C (Table 32). The standard errors of the variances were lower than the variance estimates at all sites and across sites. The variance components for all effects in the single-site and combined-site models for both MBL and MNL appear in Appendices 12 through 14.

Table 32: The additive genetic variances (above), and the additive genetic variances as percentages of the total variance (below) for branch and needle lengths on individual sites and across sites. Family 2914 was excluded across sites.

TRAIT	SITE A^1	SITE B	SITE C	ACROSS^1	ACROSS^2
MBL	4.02± 1.86**	0.00	1.69± 1.63*	1.42± 1.05 NS	2.08 ± 1.26 NS
MNL	4.80± 2.53**	2.21± 1.80*	1.98± 1.88 NS	2.52± 1.16**	1.91 ± 1.60 NS
MBL	7.20**	0.00 NS	2.76*	0.87 NS	2.52 NS
MNL	6.71**	2.96*	1.96 NS	2.42**	1.97
MBL (A^2)	6.29**				
MNL (A^2)	6.36*				

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined; * ($P < 0.05$); ** ($P < 0.01$); NS = not significant ($P > 0.05$).

The percentages of the additive genetic variance for both MBL and MNL at site A. did not change greatly with the exclusion of family 2914 from the analysis (Table 32). The family by replication interaction accounted for 7.8%, 16.47% and 8.93% of the total variance for MBL at sites A, B and C, respectively. It accounted for 13.96%, 8.97% and 2.72% of the total variance for MNL at sites A, B and C, respectively. At site A, the within-family effect accounted for 75.38% and 75.41% of the total variance in MBL and MNL, respectively. At site B, it accounted for 74% of the total variance in MBL and 78.33% in MNL, whereas at site C it accounted for 82.81% of the total variance in MBL and 81.32% MNL.

Across sites, the site effect was the largest source of variation in MBL. It accounted for 47.81% of the total variance when the three sites were considered jointly. The family by site interaction, and within family effect accounted for 5.71% and 40.18% of the total variance, respectively. For MNL, the site effect, family by site interaction, and within-family effect accounted for 17.52%, 0% and 66.86% of the total variance, respectively. Appendices 12 through 14 present the percentages of the variance components for all effects in the single-site and combined-site models for both MBL and MNL.

For MBL, the family-within-population effect was significant at sites A and C. It was not significant at site B, and across sites (Table 32). The family by replication interaction was significant at sites A ($P < 0.01$), B ($P < 0.001$) and C ($P < 0.05$). Across sites, the site effect for MBL was highly significant ($P < 0.001$). The family by site interaction was not significant. For MNL, the family-within-population effect was significant at sites A, B and across sites (Table 32). The family by replication interaction was significant at sites A ($P < 0.001$) and B ($P < 0.05$), but not at site C. Across sites, the site effect was significant ($P < 0.01$). The family by site interaction was, however, not significant. Hypotheses tests for all effects in the single-site and combined-site models for both MBL and MNL appear in Appendices 15 through 18.

For both branch and needle lengths, heritabilities were higher at site A than at the other two sites (Table 33). At site A, heritability estimates did not change drastically with the exclusion of family 2914 from the analysis. Family heritability for MNL was higher across sites than at individual sites when all three sites were involved. For all sites and across sites, the standard errors of heritabilities for both MBL and MNL were lower than the heritability estimates.

Table 33: Heritability estimates and their standard errors for branch and needle lengths on individual sites and cross sites. Family 2914 was excluded across sites.

SITE	TRAIT	h_i^2	$S.E(h_i^2)$	h_f^2	$S.E(h_f^2)$
A^1	MBL	0.32	0.12	0.60	0.15
	MNL	0.28	0.12	0.53	0.14
A^2	MBL	0.28	0.12	0.58	0.09
	MNL	0.26	0.11	0.51	0.14
B	MBL	0.00	0.00	0.00	0.00
	MNL	0.13	0.09	0.36	0.10
C	MBL	0.12	0.09	0.32	0.10
	MNL	0.09	0.08	0.31	0.09
ACROSS^1	MBL	0.07	0.04	0.41	0.08
	MNL	0.13	0.05	0.62	0.11
ACROSS^2	MBL	0.14	0.06	0.50	0.11
	MNL	0.09	0.05	0.40	0.08

A^1 -family 2914 included; A^2 -family 2914 excluded; ACROSS^1 -A, B & C combined; ACROSS^2 -A & C combined.

3.2.5 Survival

Family survival rates followed the order, site A > site B > site C. Total survival rates were, 98.13% at site A, 92.86% at site B, 87.17% at site C, and 92.23% across sites. Percentage survivals for individual families were high at all sites and across sites (Table 34). At site A, family 2926 had the lowest survival rate (88%). All other families had survival rates greater than 90%. With 64% survival, 2908 and 2927 were the families with the lowest survival rates at site B. All other families had equal or greater than 80% survival. The poorest surviving families at site C were 2902 and 2909 with 68% survival each. All other families had greater than 75% survival. Only one family (2916) did not suffer any mortality at all three sites. All other families experienced mortality at site C. With the exception of 2902, all families with the lowest survival at sites B and C did not experience mortality at site A. Notice that the differences in survival rates among families were not statistically significant (Table 34).

Table 34: Survival percentages and Chi-Square tests for Scots pine families on individual and across test sites.

FAMILY	SITE A[1]	SITE B	SITE C	ACROSS[1]
2901	100	100	92	97.3
2902	96	96	68	96.7
2903	96	100	92	96.6
2904	100	100	88	96.0
2905	100	100	84	94.7
2906	96	100	88	94.7
2907	100	92	88	93.3
2908	100	64	88	84.0
2909	100	100	68	89.3
2910	100	100	88	96.0
2911	100	100	84	94.7
2912	100	96	88	94.7
2913	96	92	92	93.3
2914	96	NP	NP	NA
2915	96	88	92	22.2
2916	100	100	100	100
2917	100	100	92	97.3
2918	96	100	88	94.7
2919	100	100	80	93.3
2920	100	92	84	92.0
2921	92	100	84	92.0
2922	100	84	88	90.7
2923	100	80	92	90.7
2924	96	76	88	86.7
2925	100	100	92	97.3
2926	84	96	96	92.0
2927	100	64	88	84.0
2928	100	83	76	85.3
2929	100	100	84	94.7
2930	100	100	96	98.7
Mean	98.1	93.2	87.2	90.8
χ^2	0.89 NS	8.83 NS	4.16 NS	4.11 NS
DF	29	28	28	28

A[1] -family 2914 included; ACROSS[1] -A, B & C combined; NP -not planted; NA -not available, NS = not significant ($P > 0.05$).

3.3 Genotype by Environment Interaction

In this study, the population by site interaction was statistically significant in height at age 4 and 5. It was not significant in height at age 6. At a family-within-population level, the family by site interaction was significant for height at age 4 through age 6. It was also significant for INC2 (Appendix 18). For height growth, the family by site interaction variance decreased from 3.67% of the total variance at age 4 to 2.5% at age 5, and then increased to 2.92% at age 6 (Appendix 14). Generally, the genotype by environment interaction was a greater source of variation than the genetic main effects in the analysis of variances when all three sites were jointly considered. The importance of the G x E interaction in height growth is also reflected in the low values of the type B genetic correlations between site pairs (Table 35).

Table 35: Type B genetic correlation coefficients between site pairs.

TRAIT	SITE A^2 & B	SITE A^2 & C	SITE B & C
H4	0.04 ± 0.34	0.65 ± 0.28	-0.27 ± 0.32
H5	0.54 ± 0.45	0.55 ± 0.29	-0.16 ± 0.36
H6	0.46 ± 0.39	0.41 ± 0.32	0.07 ± 0.40
INC2	0.36 ± 0.38	0.56 ± 0.30	0.47 ± 0.40

A^2 -family 2914 excluded

Notice that correlations were relatively higher and more consistent between sites A and C than between sites A and B and sites B and C. Also, the correlation coefficients between sites A and B, and B and C were associated with greater standard errors than the corresponding values between site A and C. This shows that family performances were more comparable at sites A and C than at sites A and B or B and C. This is in agreement with the fact that both the additive genetic variance and heritability estimates were higher and comparable at sites A and C than at site B.

3.4 Genetic and Phenotypic Correlations

With few exceptions, genetic correlations among growth traits (height, height increments, diameter, branch length) were very high at all three sites and across sites (Table 36 through 39). In reality, genetic correlations between heights (H4 through H6), diameters (D1 and D2) and height increments (INC1 and INC2) are age-to-age correlations in these traits. They show the degree with which family performances at a certain age can be predicted from their performances at previous ages. With few exceptions, age-to-age genetic correlations for absolute height were greater than 0.90. Similarly, age-to-age phenotypic correlations for height were high ($r > 0.8$). The correlations between INC1 and INC2 were high at site A ($r = 0.83$) and across sites ($r = 1.0$), but low at site B ($r = 0.34$) and site C ($r = 0.10$). At all three sites and across sites, age-to-age phenotypic correlations for height increments were less than 0.45. Genetic correlations between D1 and D2 were high at site A ($r = 0.97$) and site C ($r = 0.98$), but very low at site B ($r = 0.18$).

Diameters were highly correlated genetically with heights ($r = 0.71$ - 1.0), and genetic correlations between diameters and height increments were between 0.4 and 0.9 at site A. The corresponding correlations at site C, were 0.86 - 0.95, and 0.66 and 0.97. At both sites A and C, phenotypic correlations between diameters and heights and height increments ranged from 0.5 to 0.8. At site B, genetic correlations between diameters and heights and height increments were either greater than 1.0 or negative (Table 37). However, phenotypic correlations were high ($r = 0.60$ - 0.79), except the correlations between diameters and INC1 ($r = 0.38$). Genetic correlations between diameters and heights and height increments were not computed across sites due to zero (small negative) genetic variances for diameters. Phenotypic correlations were between 0.50 and 0.80 (Table 39).

At site A, average branch length (MBL) was highly correlated genetically (r = 0.78 - 0.95) and phenotypically (r = 0.62 - 0.81), with other growth traits. The corresponding correlations at site C were, 0.47 - 0.88 and 0.45 - 0.64. Genetic correlations between MBL and other traits were not available for site B due to zero genetic variance for MBL. Phenotypic correlations were moderate to high (r = 0.5 - 0.74). Except for INC2, genetic correlations between MBL and heights (r = 0.62 - 1.0) and between MBL and height increments (r = 0.65 - 1.0) were high a cross sites. Genetic correlations between diameters and other traits were not available due to zero genetic variances in D1 and D2. Phenotypic correlations were moderate to high (r = 0.5 - 0.91).

An interesting observation in this study is that needle length was a trait that was not strongly positively correlated genetically or phenotypically with growth traits. At sites A, B and across sites, MNL was negatively correlated genetically with all growth traits (Table 36 37, 39). Even at site C where MNL was positively correlated genetically with growth traits, the correlations were very small, except for diameters (Table 38). At all three sites and across sites, MNL was not correlated phenotypically with growth traits as judged by very small correlation coefficients (Table 36 through 39).

Table 36: Table 36: Genetic (lower diagonal) and phenotypic (upper diagonal) correlation coefficients between traits for site A[1].

TRAIT	H4	H5	H6	INC1	INC2	AINC	TINC	D1	D2	MBL	MNL
H4		0.96	0.89	0.57	0.47	0.60	0.60	0.72	0.70	0.68	-0.04
H5	1.00		0.93	0.78	0.51	0.72	0.72	0.74	0.72	0.77	-0.03
H6	0.97	0.98		0.75	0.77	0.90	0.90	0.74	0.72	0.81	0.01
INC1	0.98	0.99	0.98		0.43	NA	NA	0.56	0.55	0.73	0.01
INC2	0.78	0.80	0.91	0.83		NA	NA	0.51	0.48	0.62	0.09
AINC	0.89	0.90	0.97	NA	NA		NA	0.62	0.60	0.77	0.06
TINC	0.89	0.90	0.97	NA	NA	NA		0.62	0.60	0.77	0.06
D1	0.80	0.83	0.83	0.90	0.72	0.82	0.81		0.92	0.72	0.23
D2	0.82	0.82	0.71	0.81	0.40	0.57	0.57	0.97		0.69	0.24
MBL	0.78	0.84	0.88	0.95	0.84	0.92	0.92	0.83	0.67		0.10
MNL	-0.54	-0.65	-0.60	-0.92	-0.42	-0.62	-0.62	-0.17	-0.23	-0.53	

NA = not applicable, i.e., correlations not computed since the traits were derived from each other; thus, the correlation between them has no meaning.

Table 37: Genetic (lower diagonal) and phenotypic (upper diagonal) correlation coefficients between traits for site B.

TRAIT	H4	H5	H6	INC1	INC2	AINC	TINC	D1	D2	MBL	MNL
H4		0.90	0.83	0.27	0.47	0.45	0.45	0.76	0.74	0.50	0.04
H5	0.93		0.95	0.67	0.57	0.72	0.72	0.76	0.75	0.70	0.04
H6	0.85	0.93		0.65	0.80	0.87	0.87	0.79	0.79	0.74	0.06
INC1	-0.24	0.15	0.23		0.44	NA	NA	0.38	0.38	0.67	0.02
INC2	0.50	0.64	0.84	0.34		NA	NA	0.61	0.62	0.61	0.09
AINC	0.23	0.52	0.71	NA	NA		NA	0.60	0.60	0.74	0.06
TINC	0.23	0.52	0.71	NA	NA	NA		0.60	0.60	0.74	0.06
D1	1.92	1.18	1.19	-2.18	0.96	-0.43	-0.44		0.83	0.56	0.13
D2	1.19	0.90	1.02	-0.95	1.02	0.27	0.27	0.18		0.59	0.12
MBL	NC	NC	NC	NC	NC	NC	NC	NC	NC		-0.03
MNL	-0.24	-0.72	-0.67	-1.32	-0.42	-0.92	-0.92	-1.78	-0.85	NC	

NA = not applicable, i.e., correlations not computed since the traits were derived from each other; thus, the correlation between them has no meaning.

Table 38: Genetic (lower diagonal) and phenotypic (upper diagonal) correlation coefficients between traits for site C.

TRAIT	H4	H5	H6	INC1	INC2	AINC	TINC	D1	D2	MBL	MNL
H4		0.96	0.88	0.31	0.39	0.44	0.44	0.73	0.72	0.45	0.14
H5	1.01		0.93	0.58	0.43	0.58	0.58	0.78	0.77	0.58	0.15
H6	1.00	0.95		0.56	0.73	0.82	0.82	0.80	0.79	0.63	0.19
INC1	1.71	1.50	1.18		0.30	NA	NA	0.50	0.49	0.62	0.10
INC2	0.63	0.52	0.76	0.10		NA	NA	0.51	0.51	0.47	0.19
AINC	1.00	0.87	1.10	NA	NA		NA	0.62	0.61	0.64	0.19
TINC	1.97	0.87	1.07	NA	NA	NA		0.62	0.61	0.64	0.19
D1	0.90	0.92	0.95	0.92	0.69	0.97	0.94		0.91	0.55	0.28
D2	0.87	0.86	0.89	0.73	0.66	0.94	0.94	0.98		0.50	0.30
MBL	0.59	0.68	0.70	+++	0.47	0.88	0.88	0.47	0.16		0.09
MNL	0.34	0.35	0.30	0.14	0.02	0.08	0.08	0.49	0.74	-0.24	

NA = not applicable, i.e., correlations not computed since the traits were derived from each other; thus, the correlation between them has no meaning; +++Correlation >>> 1.0.

Table 39: Genetic (lower diagonal) and phenotypic (upper diagonal) correlation coefficients between traits ACROSS[1] sites.

TRAIT	H4	H5	H6	INC1	INC2	AINC	TINC	D1	D2	MBL	MNL
H4		0.93	0.84	0.36	0.37	0.43	0.42	0.73	0.72	0.45	0.14
H5	0.99		0.93	0.58	0.43	0.58	0.58	0.78	0.77	0.58	0.15
H6	0.74	0.92		0.56	0.73	0.81	0.81	0.80	0.79	0.63	0.19
INC1	0.93	0.97	1.18		0.30	NA	NA	0.50	0.49	0.62	0.10
INC2	-0.10	0.31	0.66	1.01		NA	NA	0.51	0.51	0.47	0.19
AINC	0.33	0.59	0.88	NA	NA		NA	0.62	0.61	0.64	0.19
TINC	0.33	0.59	0.88	NA	NA	NA		0.62	0.61	0.64	0.19
D1	NC	NC	NC	NC	NC	NC	NC		0.91	0.55	0.28
D2	NC	NC	NC	NC	NC	NC	NC	NC		0.50	0.30
MBL	0.63	0.82	0.78	1.12	0.31	0.65	0.65	NC	NC		0.09
MNL	-0.57	-0.52	-0.49	-0.42	-0.20	-0.29	-0.29	NC	NC	-1.01	

NA = not applicable, i.e., correlations not computed since the traits were derived from each other; thus, the correlation between them has no meaning; NC = not computed due to negative variances.

4. DISCUSSIONS AND CONCLUSIONS

4.1 Low Levels of Variation

4.1.1 Variation at a Population Level

The general conclusion made from the results of this study is that variation at a population level was very low. At site A, the population variance did not exceed 3% of the total variance in all traits. Even at site B where the population effect was statistically significant, the population variance did not exceed 5% of the total variance in all traits. Across sites, the population variance was less than 1% of the total variance in almost all traits.

Low levels of population differentiation in Scots pine have been reported in other studies in Europe and North America. In Michigan, Ruby (1967) found that in 19 traits of Scots pine studied, the population effect accounted for only 5% of the total variance. In Sweden, Nilsson (1992) found that the population effect accounted for 2% of the total variance. There are also reports of higher levels of population differentiation in Scots pine. King (1965a) estimated a population variance as high as 28% of the total variance. The population effect was, however, reduced to 18.8% of the total variance in one year as the population by site interaction increased. He predicted further decreases in the population effect with age of trees. King (1965b) reported even higher values of up to 43% of the total variance. Using orchard clones, Van Haverbeke (1979) found that the provenance effect accounted for 35% of the total variance in crown damage scores.

Biochemical studies have also revealed low population differentiation in Scots pine. Yazdani et al. (1985) studied variation in Scots pine monoterpenes. They found that the population effect accounted for an average of 11.6% of the total variation. In an isozyme study involving 9 populations in Sweden, Gullberg et al. (1985) found that only 0.7% of the total variation was due to population differences. The regional and within-population effects accounted for 1% and 98.3% of the total variation, respectively. I can attribute low levels of population differentiation observed in this study to either of the following hypotheses or both:

(i) Narrow Sampling Range

Generally, the populations tested in this study came from a very narrow sampling range, considered the most likely source of populations well adapted to Alberta environment, based on earlier studies (Dhir 1996 per. comm.). Except the Irkutsk RSFSR (population 8) all populations were separated by not more than 1° of latitude (Table 1). With latitudinal difference of up to 3° from other populations, population 8 is clearly distinct from all other populations. It is the poorest population in almost every trait, and far below the site averages (Appendix 2). This is why the amount of deviation of population means from the general mean is greater below than above the general mean in most of the traits.

There is a difference of up to 5° of longitude among populations in this study. However, differences in longitude cannot be expected to cause large differences in environmental conditions at the seed sources. This is because changes along longitudinal gradients on the same latitude are essentially low, unless there are large topographic and edaphic differences. This is true considering the approximate climatic conditions of the seed sources discussed in section 2.2.1 (also see Nuttonson 1950). There are no large differences in temperature and precipitation even in seed sources separated by 5° of longitude.

Factors like temperature, photoperiod, and sometimes rainfall, vary with latitude rather than longitude. However, topographic features like mountains, and large water bodies may cause variation in temperature and rainfall along longitudinal gradients. Thus, without such natural features, greater climatic changes should occur along latitudes than longitudes. Climate and other factors like vegetation that change with latitude rather than longitude are important soil forming factors (Gerasimov and Glazovskaya 1965). Therefore, unless there are large geological variations along longitudes, greater variations in soil properties are expected to occur along latitudes than longitudes. This is true for the sampling region in this study. World-wide, European Russia, the west Siberian plain, Kazakhstan, and central Asia. is the region in which latitudinal soil zonation is mostly expressed (Gerasimov and Glazovskaya 1965). As mentioned earlier, the populations in this study came from the west Siberian plain (see section 2.2.1). Also as pointed out by Wright (1976), most of the environmental factors shows greater north - south than east - west trends.

Generally, there is greater selection pressure along latitudes than longitudes. Consequently, narrow sampling along latitudes and intensive sampling along longitudes as in this study, would result in sampling of populations under almost the same selection pressure. Populations subjected to the same selection pressure cannot be expected to show large among-population variation, since they have become adapted to similar environmental conditions.

Narrow sampling along latitudes also means that the populations were short distances apart. The distance among populations has a great influence on the degree of genetic differentiation, since it influences the extent of gene exchange among populations. Without geographic barriers, short distances among populations would imply greater gene flow and vice versa. As pointed out by Wright (1943), if different regions are subjected to different selection pressures, the extent of population differentiation will depend on the amount of gene flow among populations. Sufficiently large gene flow will inhibit population differentiation, whereas restricted gene flow will promote it (Wright 1943; Slatkin 1987).

Scots pine is predominantly an outcrossing species, though with some degree of selfing (Johnsson 1976; Muller-Starck 1982; Shen et al. 1981; El-Kassaby et al. 1989; Yanbayev et al. 1989). Also, Scots pine has a long range of pollen and seed dispersal. It produces clouds of pollen that are transferred by wind for tens of kilometres (Koski 1991). It is also suggested that in areas with overlapping populations, genes from one population can spread over hundreds of kilometres through subsequent pollen and seed dispersal (Koski 1991). Therefore, large population differentiation over short distances cannot be expected in Scots pine.

Previous studies in Europe and North America, involved provenances from quite different regions, and even different countries. As a result, it was possible to observe larger levels of variation at a population level, than observed in this study. In reality, some of the variations reported in those studies can be considered regional, rather than population or provenance variations.

Wright and Baldwin (1957) and Wright and Bull (1963) suggested that there is greater variation among than within geographic regions in Scots pine. This led to the idea that variation in Scots pine is essentially discontinuous, i.e., ecotypic type of variation. Both Wright and Baldwin (1957) and Wright and Bull (1963) provided descriptions of Scots pine ecotypes, and their respective boundaries. In a paper titled, *A cline or not a cline - a question of Scots pine*, Langlet (1959) critically reviewed the publication by Wright and Baldwin (1957). He cited three deficiencies in Wright and Baldwin's data, i.e., wrong latitudinal information for some provenances, seriously unbalanced experimental design, and data analysis based on regional groupings. He argued that the data by Wright and Baldwin, clearly showed a continuous (clinal) type of variation. Langlet also cited many other studies that supported north - south clines in different quantitative traits in Scots pine. In this study, there was not sufficient information to allow study of the nature of variation in different traits.

(ii) Historical Factors

As mentioned earlier, Scots pine is the most widely distributed conifer in the world. Therefore, it is important to find out whether the amount of variation observed in the species in several studies agrees with this reality or not. With extremely large natural range, Scots pine is expected to show greater geographic variation than other species with comparatively narrow ranges. However, this is not so, since many studies in Scots pine have reported low levels of variation. Wright and Bull (1963) and Ruby and Wright (1976) gave an account of the historical factors that may affect the genetic structure of Scots pine. During the Pleistocene, the species was destroyed in much of its natural range, except on highlands (the Pyrenees, Alps, Carpathians, southwestern Europe, Scandinavian highlands, and Ural mountains). It is these remnants of the species that reestablished its present geographic range through migration. As a result, most Scots pine populations, even those separated by longer distances, have many characteristics in common, reflecting a common Pleistocene origin.

Staszkiewicz (1975) argued that during the Pleistocene, the natural range of Scots pine changed repeatedly. The species migrated southward and periodically returned north during warmer interglacial periods. Consequently, the entire Scots pine population structure was destroyed. In addition, these waves of migration allowed populations from different regions to meet and hybridize, producing populations of new and different qualities.

If both the Wright and Bull (1963) - Ruby and Wright (1976), and Staszkiewicz (1975) theories are correct, the present Scots pine population structure is the result of recent retreat to restricted areas, and recolonization through migration. Slatkin (1987) pointed out that, the greatest opportunity for migration and population subdivision to play an important evolutionary role, is in species with unstable population structures, either due to frequent extinction and recolonization of local populations or occasional large-scale changes in geographic range. Scots pine clearly fits in this model. Wright and Bull (1963) argued that, evolutionary, Scots pine is lagging behind environmental changes. Its present genetic structure does not reflect the variation in environmental conditions that exist in its entire natural range. This is because even populations from quite different environments have characteristics in common.

The first hypothesis is the most likely explanation of the low level of genetic variation at a population level observed in this study. However, the second hypothesis might also have a contributory role. Unless isolated populations, or populations separated by longer distances are compared, large levels of genetic variation at a population level in Scots pine cannot be expected.

Generally, the results of this study at a population level did not provide adequate information on the amount of genetic variation that exists in Scots pine natural range. This is because very few populations from a restricted geographic range were involved. From a tree improvement point of view, none of the tested populations can be considered the best and recommended for introduction based on its mean performance. This is because except population 8, all populations differ by less than 5cm at sites, A and C and 10cm at site B in most of the traits. Such differences can be expected by chance alone. It is recommended that future studies should involve many populations sampled along latitudinal gradients. The clear differences between population 8 and the rest of the populations show that this study could have benefited more if more sampling was done along latitude than longitude.

4.1.2 Variation at a Family Level

Like variation at a population level, variation at a family level in this study can be considered low. On individual sites, the family-within-population effect accounted for not more than 8% of the total variance in all traits. It accounted for less than 3% of the variance across sites. In the experiment involving interprovenance hybrids, Nilson (1992) found that the family effect accounted for 5% to 13% of the total variance. There are, however, not many reports on the percentages of the variance at a family-within-population level in the Scots pine literature. Thus, there is not enough information to compare with the results of this study.

The low level of genetic variation in this study may be due to a lack of strong family differences within Siberian populations of Scots pine. It is also possible to observe low genetic variation if sampling of the families followed specific criteria that introduced uniformity in the test material. Although it is known that families used in this study were sampled at random (Dhir 1996 pers. comm.), biased sampling cannot be ruled out since seeds were collected by the third party.

4.2 Performance at Individual Sites

4.2.1 Performance at a Population Level

As mentioned earlier, height growth was higher at site A than site B, but diameter growth was higher at site B than site A. This might be due to competition at site A, which did not exist at site B. At site A, competition for light between experimental trees and herbs and shrubs might have promoted height growth, thus limiting the resources allocated to diameter growth. At site B, there was essentially no competition for light. Consequently, trees could allocate more resources to diameter, branch and even needle growth. This is not unexpected, since even under natural conditions solitary trees tend to be larger in diameter, shorter, and bushier than trees in closed stands (Ford 1976). In Scots pine for example, trees in closed stands attain heights of 40m or more, while solitary trees rarely exceed 15 - 20m. Also, solitary trees have more branches per whorl, and wider crowns than trees in closed stands (Przybylski 1975). Watering and fertilization at site B might also have contributed to diameter growth.

Average height increments were different from absolute height growth. Height increments were greater at site B than site A, which is just the opposite of absolute heights. In this study, height increments were assessed as the differences between H4 and H5, H5 and H6, and H4 and H6. It is possible that, between age 4 and 6 was a period during which competition between experimental trees and herbs and shrubs at both sites A and C became strong. As a result, the rates of growth in this period were lower at sites, A and C than site

B. Growth rates might have been higher at sites, A and C than site B before the start of competition. This is true since at age 4, total height (H4) was the lowest at site B, showing that site B had the poorest growth trend initially. Also, site B was fertilized, whereas sites A and C were not. Therefore, the take over of site C by site B in H5, H6, and height increment, and of site A by site B, in height increment, can be explained by a combined effect of competition at sites A and C, and fertilization at site B. Notice that at all three sites there was no inter-tree competition, since experimental trees were still far apart at the time of assessment, and crown closure may not occur in the next four years.

Survival on the three sites also deserves a brief comment. Both sites, A and C occur in the Lower Foothills Subregion, which is characterized by high summer precipitation, mild winters, and organic poorly drained soils (Anonymous 1994). Site B on the other hand. occurs in the Central Parkland Subregion with low precipitation and poor sandy soils. The rate of survival is, therefore, expected to be higher at sites A and C, because of favourable environment than at site B. However, in this study survival was higher at site B than site C. Survival at site B might have been enhanced by watering in the first two years of field establishment. On the other hand, a comparatively low survival at site C may be due to post-establishment tree mortality due to competition and insect damage.

4.2.2 Performance at a Family Level

For all assessed traits, the percentages of the additive genetic variance and heritability estimates at site B, were lower than the corresponding values at sites A and C. Besides low additive genetic variances, low heritability estimates at site B might be due to:

(i) High Values of Non-genetic Variances

The family by replication interaction and within-family variances at site B were much larger than the corresponding additive genetic variances (Appendix 10). In H6 for example, the family by replication interaction and within-family variances were 608% and 3071% of the additive genetic variance, respectively. The corresponding values were 149% and 1012% at site A, and 142% and 1277% at site C. Since the family by replication interaction and within-family variances were involved in computing heritabilities, heritability estimates should be the lowest at site B. Large standard errors of the additive genetic variances at site B can also be attributed to excessively large family by replication and within-family effects, since the mean squares of both effects were involved in computing the standard errors of the genetic variances. High family by replication interaction might be a result of within-site heterogeneity with respect to soil and moisture, and their influence on microclimate of the trees (Yeh and Rasmussen 1985). On the other hand, variability among trees in open-pollinated families might be an indicator of many effective pollen parents (Yeh and Rasmussen 1985).

(ii) The Population Effect

There was a considerably large population effect at site B that was not expressed at sites A and C (Appendix 10). In H5 for example, the variance component for the population effect was greater than the additive genetic variance. In H6 it was 50% of the additive genetic variance. The percentages of the additive genetic variance and the population variance in both H5 and H6, were almost equal (Appendix 12). At both sites A and C, the population effect accounted for 0% of the total variance. Figures 3 through 5 show that families tended to cluster in family groups at site B, but not at sites A and C.

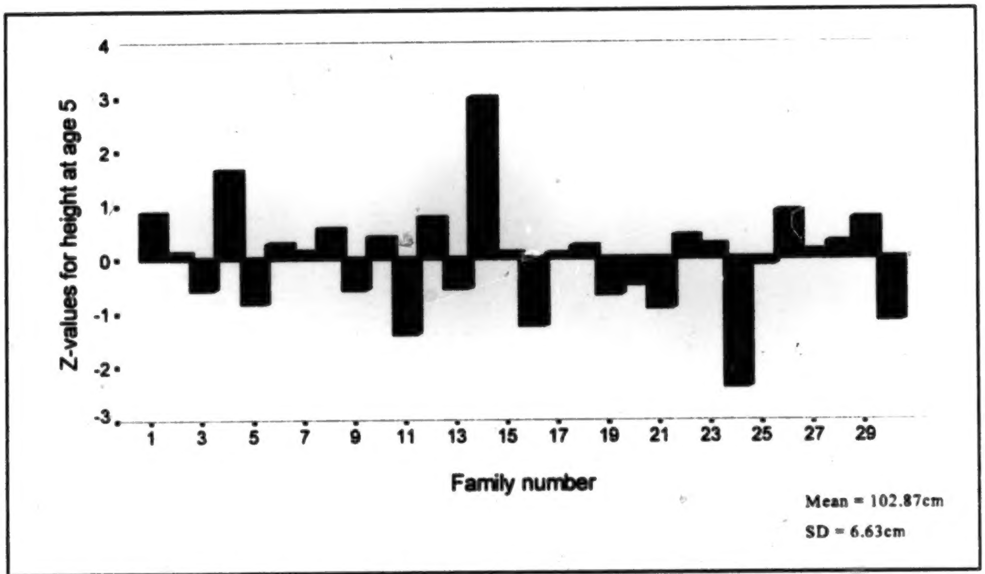

Figure 3: Standardized deviations of family means from the site mean for H5 at site A

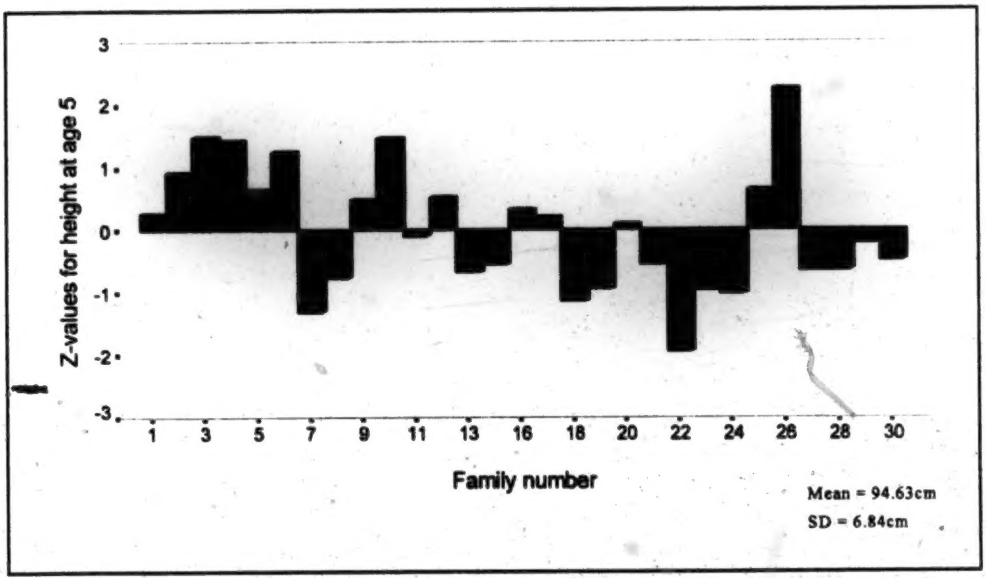

Figure 4: Standardized deviations of family means from the site mean for H5 at site B

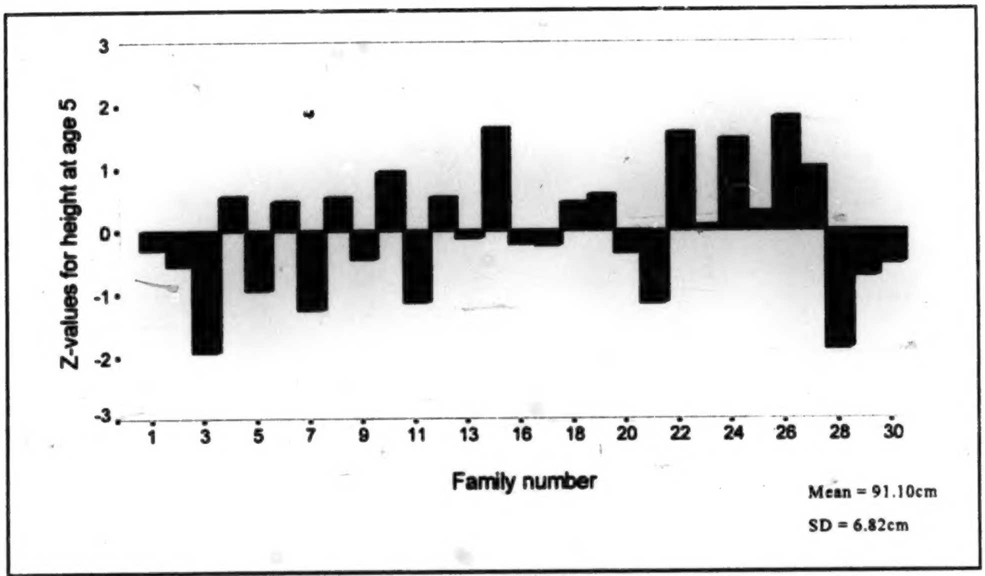

Figure 5: Standardized deviations of family means from the site mean for H5 at site C

In all three figures, the means and standard deviations used to standardize the data are indicated. Figure 4 shows that families 2901 through 2906 from population 4 are grouped together above the mean at site B, but randomly scattered at sites A and C. Similarly, most of the families in population 2 (families 2916 through 2925) are grouped together below the mean at site B, but not at sites A and C. There are also groupings of families in other populations at site B that are not reflected at sites A and C. This is true for all traits at site B, except INC1, the only trait in which the population effect had a negative variance.

The existence of a population effect at site B that was absent at sites A and C, shows that site B is ecologically a different environment from both sites A and C. The additive genetic variances at site B might appear small because the population variances and the additive genetic variances (family-within-population) were successfully separated. On the other hand, the additive genetic variances at sites A and C might appear large because they remain confounded with the population variances. Judging from the amount of the population and population by replication interaction variances at the three sites (Appendix 10), if the population effect was removed in the single-site model to confound the population variance with the additive genetic variance, and population by replication interaction with family by replication interaction variances, heritabilities would have been higher at site B than at sites A and C.

(iii) Site Management

Site management might also be responsible for the differences in the expression of family differences at the three sites. Lack of competition at site B might have allowed all families to flourish, thus obscuring family differences, while allowing non-genetic sources of variance to play a greater role. Competition between experimental trees with herbs and shrubs at sites A and C might have allowed families and individual trees with greater growth potential to do better than those with low growth potential. This would promote greater family differences than environmental differences. This is possible since individual plants possess genetic homeostasis (inborn self-regulating mechanisms) that allows them to adjust to environmental conditions that prevail at any particular time (Lerner 1954). It is also known that the ability to adapt to environmental changes requires a considerable genetic variance (Levins 1968; Pease et al. 1989). Therefore, it is possible for trees in this trial to express greater additive genetic variance in highly competitive environments of sites A and C than in the competition-free environment of site B. This should be reflected in the magnitude of single-site heritability estimates.

4.2.3 Hypotheses Testing

In this study, the family-within-population effect was statistically significant in most of the traits at sites A and C. It was not significant at site B and across sites when all three sites were involved in the analysis. In this study, random effects statistical models were used on individual sites and across sites. With these models, the appropriate denominators for testing the significance of the family effect are the mean squares of the family by replication interaction on individual sites, and family by site interaction across sites (Ott 1993). Thus, lack of statistical significance of the family-within-population effect at site B, was largely due to large family by replication interactions in addition to low family effects expressed at this site. Similarly, the family-within-population effect was not significant across sites when all three sites were involved in the analysis, due to large family by site interaction in addition to low family effect expressed across sites. This is obvious since at site B, the family effect was significant only for traits in which the genetic variance was larger than the corresponding family by replication interaction variance. Similarly, the family effect was significant across sites only for traits in which the genetic variance was larger than the corresponding family by site interaction variance (Appendix 10, 11, 15, 16, 17, 18).

4.3 Time Trends in the Population and Genetic Variances

In this study, time trends in the population and additive genetic variances can be observed only in height, height increments and diameter. These are the traits with measurements of more than one growth season. Height growth will be used as an example in discussing the time trends in the population and additive genetic variances. At site A, the population variance increased from 2% of the total variance at age 4 to 2.6% at age 6. The percentage of the population variance decreased from 4.9% at age 4 to 3.3% at age 6 at site B. Across sites, the percentage of the population variance increased from almost 0% at age 4 to 1% at age 6.

With family 2914 at site A, the percentage of the additive genetic variance increased from 7.04% of the total variance at age 4 to 7.36% at age 6. Without family 2914, the percentage of the variance dropped from 4.2% at age 4 to 3.33% at age 5, and thereafter increased to 4.81% at age 6. At site C, the additive genetic variance increased from 7.36% at age 4 to 8.04% at age 5, but then dropped to 6.03% at age 6. The most drastic change in the percentage of the additive genetic variance occurred at site B. Here, the variance decreased from 5.59% at age 4 to approximately 2.5% at both age 5 and 6. There is no explanation for this 55% decline in the percentage of the variance in one growth season and its subsequent stabilization.

Generally, the fluctuations in the percentage of the population and additive genetic variances observed in this study are small. They are also not unique to the Scots pine material used in this study. Studies have revealed similar fluctuations in other conifers. In Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) for example, Namkoong et al. (1972) found that at age 5, the family variance accounted for 10% of the total variance. After age 40, it accounted for 0% of the total variance. Large fluctuations in the family variance in a short period were also observed in interior spruce (*Picea glauca* (Moench) Voss and *P. engelmannii* Parry) in British Columbia (Kiss and Yeh 1988). In Loblolly pine (*Pinus taeda* L.), Foster (1986) found that the family variance accounted for 35%, 21%, 23% and 29% of the total variance in survival at age 1, 8, 15 and 27, respectively. Family variance decline was also observed in ponderosa pine by Namkoong and Conkle (1976). Age-to-age correlations for height, height increments, and diameter in this study are shown in Table, 36 through 39.

4.4 Heritabilities

4.4.1 Individual Sites vs Combined Sites

Heritability estimates were higher on individual sites than across sites, except at site B. This is not unexpected since additive genetic variances estimated on a single-site basis contain the family by site (G x E) interaction variances. Thus, single-site heritabilities were biased upward (Comstock and Moll 1963). Separation of the G x E interaction variance from the additive genetic variance reduces the size of the numerator while increasing the size of the denominator in heritability formulae. This reduces heritability estimates across sites compared with single-site heritabilities. Also in this study, the residual variance (replication-within-site by family-within-population) was much greater than the genetic variance in all traits (Appendix 14). In heights for example, the residual variance was 261%, 506%, 732% of the additive genetic variance in H4, H5 and H6, respectively. Thus, large residual variances were also responsible for the low heritabilities across sites. It should be noted that only in traits such as INC1 and MNL where either the G x E interaction variance, residual variance or both were small, did heritabilities across sites exceed or equal heritabilities at sites A and C. Heritability values across sites were predominantly larger than those of site B, possibly because of a combination of factors already described (section 4.2).

As already mentioned, site B appears to differ ecologically from both sites A and C. Its removal from the analysis across sites increased the genetic variance, and reduced the ratio of the G x E interaction variance to the additive genetic variance. This increased heritability estimates across sites. Therefore, the uniqueness of site B was also responsible for large values of non-genetic sources of variances, and low heritability estimates across sites.

4.4.2 Comparison with Other Studies

One important question is how the findings from this study compare with findings from other Scots pine studies conducted elsewhere. Indeed, there are more similarities than there are differences in the results of this study with results in Europe and the United States. Low, medium, and high heritability values have been reported for growth variables in Scots pine. In a series of height assessments in Germany, Krusche et al. (1980) found that individual tree heritabilities were less than 0.4 on individual sites and across sites. Only in two extreme cases (h^2 = 0.6 and 0.85) did heritabilities exceed 0.4. Ehrenberg (1963) estimated heritabilities of 0.41 and 0.85 for height in Sweden. Poykko (1982) and Haapanene and Poykko (1993) found that heritabilities for heights in Finland were between 0.32 and 0.95.

In Michigan, Wright (1963) estimated family heritability for 2-year height on individual population basis. He found heritability values of 0.816 and 0.803 for the Germany and Belgian populations, respectively. Scots pine studies have shown lower heritability for diameter than height, e.g., 0.18 - 0.43 (Poykko 1982), 0.21 (Haapanene and Poykko 1993). and 0.15 (Krusche et al. 1980). Wright (1963) found heritability of 0.55 and 0.51 for the Belgian and Germany populations, respectively.

In this study, heritabilities were in the low to medium range for all growth-related traits and needle lengths. Individual tree heritabilities have a lower limit of 0.01 in INC1 across sites without site B, and an upper limit of 0.34 in H5 at site C. Family heritabilities have a lower limit of 0.06 in INC1 across sites without site B, and D1 at site B, and an upper limit of 0.62 in MNL across sites with all three sites. On individual sites, low heritabilities in this study, may be an indication of low genetic differences (low additive genetic variance) among families. At site B in particular, low heritabilities may also be the result of large family by replication interactions. Across sites, both low additive genetic variances and high G x E interaction and residual variances were responsible for low heritability estimates. It is also possible to obtain low heritabilities if sampling of families was conducted with some bias. This would reduce the additive genetic variances, and consequently, heritabilities.

4.4.3 Implications to Selection and Breeding

Having estimated genetic variances and heritabilities, the implications of these genetic parameters to selection and breeding of Scots pine in Alberta need to be discussed. As already mentioned, family heritabilities in this study were more important than individual tree heritabilities. Therefore, family selection is more important in this study than mass selection. According to Falconer (1960), family selection (selection of whole families based on the mean phenotypic value of the family) is the most effective selection method when heritability of a trait is low. Here environmental factors contribute greatly to the phenotypic variance.

The effectiveness of family selection in this study, however, is dependent upon the role of maternal effects, especially the size of the seeds in influencing family differences. According to Falconer (1960), environmental variations common to members of the family reduce the effectiveness of family selection. This is because they make members of the same family resemble each other more than they resemble members of other families. Therefore, maternal effects lead to overestimation of the genetic variance and heritability, thus making family selection ineffective.

In Scots pine, there are reports of maternal effects being persistent beyond 5 years. Reich et al. (1994) studied the influence of seed weight on height in 24 populations in the 1982 IUFRO series in Europe. They found that seed weight significantly influenced tree height in central European populations up to 5 years from planting. In other populations, however, the effect of seed weight on tree height disappeared in 2 years from planting. In central European populations, however, the correlation coefficient between seed weight and tree height dropped by more than 50% between age 5 and 7 from its value between age 1 and 4. This was not so in 5 northern populations (3 Russian, 1 Latvian, 1 Swedish) in which the coefficient remained high (r = 0.89) at 7 years from planting. Such results suggest that maternal effects can persist beyond 7 years especially in slow growing populations of Scots pine. In a phytotron study, Dormling and Johnsen (1992) found that the effects of parental environment of the progeny to the seedling height and height increments disappeared in the second growing season.

In this study, it is not possible to conclude with certainty whether seed size influenced family performances or not. This is because seed weight data were available for only half of the families tested (Appendix 21). However, from the few data available on seed weight, it appears that seed size had no relationship with family height growth. For example, family 2912 with 4.94gm/1000seeds was above the mean in H4 through H6, at all three sites. On the contrary, family 2930 with 7.46gm/1000seeds was below the mean in H4 through H6, at all sites. At site B, family 2929 with 7.41gm/1000seeds was below the mean in H4 through H6, whereas families 2901 through 2906 with less than 7.0gm/1000seeds were above the mean in H4 through H6. Pearson correlation coefficients between 1000seed weights and family mean heights for the 16 families whose seed weight data were available show no linear relationship between family performances and seed weight (Table 40).

Table 40: Pearson correlation coefficients between 1000 seed weight and family means for heights.

SITE	H4	H5	H6
A	0.1144	0.0534	0.1275
B	-0.2366	-0.1938	-0.3342
C	0.2327	0.0879	0.2494

All correlations are not significant ($P > 0.05$)

These low correlation coefficients suggest that maternal effects did not influence family performances in this study. Therefore, parameters estimated in this study reflect genetic variation, rather than variation in environment common to members of the same family. Notice, however, that the observation on maternal effects is based on data for only half of the families tested. It is not known what the situation would have been if seed weight information were available for all 30 families involved in the study. Thus, one can take precautions by adopting a combined selection to make use of both family and within family variation.

The effectiveness of family selection also depends on the number of individuals per family tested (Falconer 1960). According to Falconer, the correspondence between the mean phenotypic value and mean genotypic value increases as the family size becomes larger. In this study, 25 individuals per family were tested on each site. The number of individuals per family needed to give reliable estimates depends on the heritability of a trait, and equals, $\frac{4}{h_i^2}$

for half-sib families (Falconer 1960). Where h_i^2 refers to individual tree heritability for the trait. This means that the lower the heritability, the larger the number of individuals per family needed to give reliable heritability estimates and vice versa. With individual tree heritability of 0.15 for example, 27 trees per family would be needed per site. In this study, individual tree heritability on individual sites was greater than 0.15 for most of the traits. Thus, 25 trees per family used in this study on individual sites were enough to guarantee reliable heritability estimates.

The limitations of family selection in this study obviously come from the limited number of families available for selection. According to Zobel and Talbert (1984), 25 to 40 clones are needed to establish a seed orchard, and after that roguing the orchard to 20 or fewer best clones. With family selection, clones imply the families being selected for inclusion in the seed orchard. Therefore, there are not enough families to select from with an appropriate selection differential, since only 30 families are available. Here, family and within-family selection can be combined to obtain the material for the seed orchard. According to Zobel and Talbert (1984), this selection approach works well. when heritabilities are low.

From the available material, 5 best families across sites should be selected. and from these five families, 25 best trees should be selected for the seed orchard. Notice, however, that since very families are selected, there will be many genetically related clones in the seed orchard. This may increase the level of inbreeding in the orchard. Thus, while the present material is being used, effort should be made to secure more material to broaden the genetic base.

4.5 Practical Implications of G x E Interaction

Plant breeders have two options: (1) developing genotypes adapted to a wide range of environments (low G x E interaction), or (2) developing genotypes adapted to specific environments (greater G x E interaction) (Comstock and Moll 1963). Both options require characterization of environments with respect to G x E interactions (Burdon 1977). According to Burdon, in the first option one need to recognize a few environments which singly or in conjunction allow for effective screening of genotypes that are broadly adapted. In the second option one need to delimit appropriate groups of environments and then identify which specific environments within groups provide the best resolution of genetic differences.

G x E interaction may occur either when genetic variances expressed by a trait in different environments differs greatly, or when ranking of genetic groups (e.g. families) differs in different environments (Robertson 1959). Of the two causes of G x E interaction. it is the alteration in ranking of genotypes among environments that is the basis for dividing environments into separate breeding zones in any tree breeding programme (Burdon 1977).

In this study, low type B genetic correlations suggest that ranking of families in order of merit changed at the three test sites. This is also obvious when the amount of deviation of family means from the general mean is considered at the three sites in traits with significant G x E interaction in the analysis of variances. Height at age 4 (H4) will be used as an example of traits with significant G x E interaction. Appendix 19 shows that family 2903 was 6.9% and 15.2% below the mean at sites A and C, respectively, but it was 12.69% (second best) above the mean at site B. Family 2905 was 5.63% and 9.08% below the mean at sites A and C, respectively, but it was 9.77% (fifth best) above the mean at site B. Family

2922 was 16.31% (poorest) below the mean at site B, but it was 11.3% (third best) above the mean at site C. It was only 2.09% above the mean at site A. Family 2924 was 15.92% (poorest) below the mean at site A, but it was 13.02% (second best) above the mean at site C, and 7.79 below the mean at site B. These families and others not mentioned, are suitable for improvement purposes only in environments in which they display excellent performance. They are not suitable for a broad range of environments.

The change in family ranking at the three sites is also evident from the very low Spearman's rank order correlation coefficients of family means between pairs of test sites (Table 41). Notice that correlation coefficients between site pairs are predominantly very small, showing that family ranks were different on the three test sites. Table 41 also shows that correlation coefficients were relatively larger between sites A and C, than between sites A and B or sites B and C.

Table 41: Spearman's rank order correlation coefficients of family means for the three test sites.

TRAIT	SITE A & B	SITE A & C	SITE B & C
H4	0.03	0.39	-0.16
H5	0.14	0.34	-0.09
H6	0.21	0.22	0.09
INC2	0.06	0.34	0.18
D1	-0.11	0.14	0.03
D2	-0.22	0.19	-0.05

There were, however, few (17%) families that showed a considerable stability on the three test sites. Families 2904, 2906, 2910, 2912, and 2926 were above the mean at all sites in H4 through H6 (Appendix 19). These stable families are suitable for a wide range of environments, though their degrees of expression differ on the three sites, and they are not necessarily the best on an individual site basis.

As opposed to annual crops, forest environments are permanent features, since little can be done to change their climate, topography and soil properties. Moreover, forest environments are more-permanent than genotypes that grow on them, since new and different genotypes can be produced every time needed. Therefore, it is logical to focus on the role of environments rather than the genotypes in creating G x E interactions (Burdon 1977). Type B genetic correlations provide the opportunity for characterizing the test environments rather than genotypes. They are, therefore, useful in deciding which environments give the best screening of genotypes (Skroppa 1984). Furthermore, the quantification of G x E interactions in terms of type B genetic correlations is more of a measure of the practical significance of G x E interactions rather than the statistical significance of the results (Robertson 1959).

In this study, sites A and C were the best in screening genotypes. On these sites, additive genetic variances and heritabilities were much higher than at site B. Furthermore, genetic parameters at sites A and C were comparable, but not at site B. Apparently, strong G x E interactions observed in this study, especially in height growth were largely due to the differences between sites A and C on one hand and site B on the other. This is why removal of site B from across site analysis increased both the additive genetic variances and heritabilities. The reliability of sites A and C in providing better estimates of genetic parameters is to be taken with caution because of possible confounding of the population variance and the additive genetic variance (see section 4.2.2 ii).

There are, however, considerable differences between sites A and C that might be of practical importance. Robertson (1959) suggested that a type B genetic correlation of 0.8 with a standard error of 0.2 is an absolute minimum for a G x E interaction to be of biological and agricultural significance. In this study, type B genetic correlations between sites A and C were far below 0.8, and their standard errors were greater than half the correlation coefficients. This suggests that despite their similarities relative to site B, their differences are too great to be considered one and the same breeding zone.

It is also important to quantify the genotype by year interactions besides G x E interactions (Allard and Bradshaw 1964). This is because they reflect fluctuations in environment due to unpredictable factors such as temperature and rainfall distribution, the factors subject to random changes from year to year. In forestry, however, genotype by year interactions may not be important, since the effects of year-to-year climatic fluctuations are averaged over a long rotation (Burdon 1977). Furthermore, genotype by year interactions cannot be used to select genotypes adapted to particular years, since future environments cannot be accurately predicted in advance (Bulmer 1980). In this study, there are likely to be some genotype by year interactions, as there were fluctuations in G x E interactions from one year to another. However, considering the arguments by Burdon (1977) and Bulmer (1980), genotype by year interactions are not expected to affect breeding decisions made from this study.

Studies at the provenance level in Scots pine have revealed significant genotype by environment interactions in height, needle length, and needle colour, though the provenance by site interaction variances were lower than the provenance variances (King 1965a, 1965b). In both cases, it is the provenances from Scandinavia, Spain, Greece and Turkey that changed performance from site to site and year to year. Mergen et al. (1974) studied provenance by temperature interaction in the growth chamber with Scots pine, white spruce, sitka spruce and jack pine. They found no significant interaction in Scots pine, though it existed in the other three species. In the IUFRO 1938 provenance trials, provenances from Scandinavia exhibited greater provenance by site interaction, whereas provenances from the lowlands of central Europe did not (Giertych 1991). According to Giertych, provenances from central Europe, especially the Baltic countries, and north and western Poland, displayed superior growth wherever planted. They did better in Scandinavian countries, southern and eastern Europe, and the United States, e.g., Michigan.

Studies have shown that strong G x E interactions are more common in provenances from extreme parts of the species natural range than those from the centre of the range. Also, provenance from regions of low growth potential display greater G x E interactions than provenances from regions of high growth potential (Mergen et al. 1974). This is because provenances from the optimal growth zone of the species exhibit higher physiological homeostasis than those from marginal and/or rigorous natural environments (Ledig 1970) cited by Mergen et al. (1974). Consequently, provenances from the centre of the species range are broadly adapted (low G x E interaction) to a wide range of environments than those from extreme parts of the species range. This phenomenon may explain why in Scots pine, strong G x E interactions occur in provenances from northern and southern Europe. Both regions represent areas of low growth potential and harsh environments in Scots pine.

It is also known that due to individual and population buffering, highly genetically variable populations exhibit lower G x E interaction than populations with low genetic variability (Allard and Bradshaw 1964). Scots pine from the lowlands of central Europe, is considered more genetically variable than Scots pine from other parts of the species' range (Giertych 1979). According to Giertych, after the final glaciation, Scots pine and other vegetation returned to central Europe westward from the central Russian plains and northward across the mountain ranges. These two waves of migration met in the lowlands of central Europe, where they created a very rich gene pool with abundant heterozygosity. Thus, provenances from this region should show little or no G x E interaction.

The strong G x E interaction observed in this study can probably also be explained in terms of both low physiological homeostasis and low genetic variability. Siberian populations have been ranked below average in most provenance studies conducted outside their locality (Giertych 1991). Thus, Siberian populations can be considered as belonging to a region of low growth potential similar to populations from the extreme south and north of the species' natural range. Furthermore, the populations used in this study originated from the region outside the main distribution of Scots pine (Figure 1). Such populations are likely to exhibit strong G x E interaction, as do populations from the extreme north and south of Scots pine range, and other regions of scattered distribution.

In this study, the level of genetic variability at the population and family level was low (see section 4.1). This might mean a lack of both individual and population buffering, that makes populations and families respond drastically to environmental changes, and thus, strong G x E interaction. However, because the populations in this study came from a very narrow sampling range, low genetic variability in Siberian populations cannot be confirmed. Thus, low genetic variability is less likely an explanation of the strong G x E interaction observed in this study.

At this point, some general remarks can be made on the implications of the G x E interaction to selection and breeding of Scots pine in Alberta. Shelbourne (1972) suggested as a rule of thumb that, when a G x E interaction component reaches 50% or more of the genetic component (provenance, family, clone) of variance, the effects of the G x E interaction are likely to be serious on gain from selection and testing. In this study, the family by site interaction variance was much larger than the additive genetic variance for all traits with significant G x E interaction in analysis of variances. The family by site interaction variance was 418.4%, 115.9%, 221.4% and 153.7% of the additive genetic variance in H4, H5, H6 and INC2, respectively. Thus, in this study, G x E interaction was a more important source of variation than the additive genetic variance. Also in this study, there were fewer stable and superior families than families that changed ranks on different test sites. The following options can be adopted to cope with a strong G x E interaction:

(i) Treat the three sites as different breeding zones and use superior families on each site. Although this option would ensure the highest genetic gain, it would fragment the breeding programme and increase operational costs, since each breeding zone would need an independent seed orchard.

(ii) Treat sites A and C as one breeding zone and site B as a separate breeding zone. This stems from the fact that site B is much different from the other two sites, and sites A and C are comparable, though gain can be maximized by separating them (option i).

(iii) Treat all three sites and other related sites as one breeding zone and use families that are superior and stable across sites. This is the cheapest option in terms of financial resources and labour, since only one seed orchard is needed. However, this option requires acquisition and testing of many more families, since out of the 29 families tested in this study, only five stable and superior families were found. Also, due to strong G x E interaction observed in this study, suitable families can only be identified through progeny testing on several sites. This, and the need to maintain greater selection differentials, demand a much larger progeny test than the one used in this study.

The results of this study should, however, be taken with caution, since the trees are still young. It is possible that the pattern of the additive genetic variance and G x E interaction variance may change as trees get older. Also, the major use of Scots pine in North America is Christmas trees rather than timber production. This is also likely to be the case in Alberta. Therefore, there is a need to study the pattern of the additive genetic variance and G x E interaction in Christmas tree traits, e.g., crown size and shape, winter needle colour, indoor needle retention, and stem form. Studies of the G x E interaction in Christmas tree traits may cast a different picture from the one revealed by timber-related traits, and thus lead to different breeding decisions.

4.6 Practical Implications of Genetic Correlations

Earlier studies showed equally high age-to-age correlations in Scots pine. Wright and Baldwin (1957) found that the correlation between nursery seedling height and field height at age 17 was 0.933. This is, however, likely to be a phenotypic correlation, since it was estimated in a provenance study with bulk seedlots. It, however, suggests that height at older ages can be predicted from nursery seedling height. In Germany, Krusche et al. (1980) found that the correlations between 6-year and 11-year height on two study sites were 0.95 and 0.91. The correlations between 3-year and 11-year heights at the same sites, however, were lower (0.34 and 0.68, respectively).

Both age-to-age genetic and phenotypic correlations estimated in this study were higher than those found in other studies. However, they are based on short intervals, i.e., age 4 to 6 for height and age 1 and 2 for diameter. Therefore, they are likely to be higher than would be expected if longer intervals were involved. It is logical to assume that height or diameter at any age is a reflection of tree growth in the last growth season. Thus, the predictability of mature age performance from early age performance in Scots pine in Alberta, need confirmation by more studies that will allow long interval correlations.

This study shows that height, diameter and branch length were strongly positively correlated genetically. This shows that improvement in height would also result in improvement in diameter and, consequently, improvement in volume production. On the negative side, improvement in height and diameter could result in trees with big branches, and thus big knots. This could reduce the product quality where knot-free timber is needed.

Other studies have shown equally high correlations between height, diameter and volume in Scots pine. In Germany, Krusche et al. (1980) found that the genetic correlations between height and diameter in Scots pine were between 0.5 and 0.96. The correlations became stronger as trees became older. Eriksson et al. (1987) estimated a genetic correlation of 0.7 between height and diameter in Sweden. Both Eriksson et al. (1987) and Kohlstock and Schneck (1992) found that genetic correlations between height and tree volume in Scots pine were greater than 0.9. The correlation between diameter and tree volume was estimated at 0.93 (Eriksson et al. 1987). There are no accounts of genetic correlations between tree height and branch length in the Scots pine literature for comparison with the correlations observed in this study. However, studies at a provenance level clearly show that branch size varies with tree growth-rate (see section 1.2.3.1.2 ii).

In this study, needle length was negatively correlated genetically with growth traits, suggesting that fast growing families had short needles and vice versa. This is the case for some families and not for others, as exemplified by MNL and H5 at site B (r = 0.72) (Figure 4 and 6).

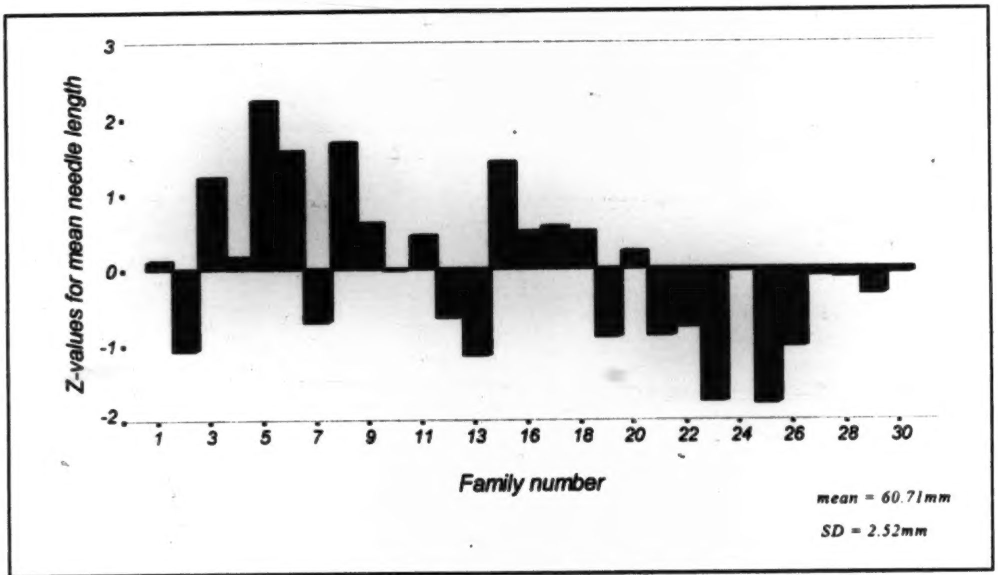

Figure 6: Standardized deviations of family means from the site mean for MNL at site B

Figures 4 and 6 show that families 2902, 2908, 2912, 2915, 2918, 2925, and 2926 (the first two digits in family accession numbers, i.e., 29 have been dropped in the figures), were above the site mean in H5, but below the site mean in MNL. The best family in height (2926) had the shortest needles. Furthermore, families 2924, 2927, 2928 and 2930, which were slightly below the mean in H5, were very close to the mean in MNL. Family 2910, the second best in H5, was exactly on the mean in MNL. A careful examination of the two figures confirms that all families changed in ranking for height and needle length. Similar patterns can be observed in all other traits that were negatively correlated genetically with MNL.

The small positive correlations between needle length and growth traits at site C, suggest a lack of genetic relationship between needle length and growth traits. This supports the argument by Ruby and Wright (1976) that needle length and growth potential in Scots pine might have no direct causal relationship. However, the results of this study confirm overwhelmingly, a negative relationship between needle length and growth traits. Negative genetic correlations between needle length and growth traits suggest that the longer the needles the lower the growth potential and vice versa.

The existence of a direct causal relationship between needle length and growth traits can be a tool for indirect early selection for economic traits. Scots pine needles have a life span of 3 years (Watson 1947). Assessment of fully-mature 3-year old needles can be a basis for identification of superior and inferior families and individual trees. This can shorten the breeding cycle for height and diameter that require mature trees to assess with certainty. However, the Scots pine literature does not provide information on the genetic correlations between needle length and other traits, with which to compare the results of this study. Thus, results of genetic correlations between needle length and growth traits should be considered preliminary, pending further investigation.

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APPENDICES

Appendix 1: Accession numbers of seedlots used in this study. Numbers assigned to seedlots in figures are shown in brackets.

Population	Latitudes	Longitudes	Altitude (m)	Fam. Acc. No.
1 Kemgrovo, RSFSR, USSR	54° 85' N	85° 19' E		
				2926 (26)
				2927 (27)
				2928 (28)
				2929 (29)
				2930 (30)
2 Kemgrovo, RSFSR, USSR	54° 00' N	86° 20' E		
				2916 (16)
				2917 (17)
				2918 (18)
				2919 (19)
				2920 (20)
				2921 (21)
				2922 (22)
				2923 (23)
				2924 (24)
				2925 (25)
3 Novosibirsk, RSFSR, USSR	54° 08' N	81° 16' E		
				2911 (11)
				2912 (12)
				2913 (13)
				2914 (14)
				2915 (15)
4 Novosibirsk, RSFSR, USSR	55° 05' N	82° 45' E		
				2901 (1)
				2902 (2)
				2903 (3)
				2904 (4)
				2905 (5)
				2906 (6)
5 Novosibirsk, RSFSR, USSR	54° 08' N	81° 15' E		
				2907 (7)
				2908 (8)
				2909 (9)
				2910 (10)
6 Kemgrovo, RSFSR, USSR*	54° 00' N	85° 20' E		2899
7 Novosibirsk, RSFSR, USSR*	55° 05' N	82° 45' E		2898
8 Irkutsk, RSFSR, USSR*	52° 15' N	84° 20' E		2897
Chickadee Creek**	54° 13' N	115° 54' W	829	2313
Swartz Creek**	53° 30' N	116° 10' W	1090	2658

* Bulk Scots pine seedlots. ** Bulk local pine seedlots.

Appendix 2: Population means and the number of observations (N) per population used in the analysis at individual sites and across sites.

TRAIT	POPULATION	A		B		C		ACROSS	
		Mean	N	Mean	N	Mean	N	Mean	N
H4	1	79.09	118	60.31	106	72.26	107	70.87	331
	2	76.20	242	57.99	228	73.13	206	69.12	676
	3	80.91	119	59.03	94	72.58	88	69.82	277
	4	77.21	165	65.75	170	69.11	141	70.72	467
	5	78.15	100	59.14	88	71.62	81	69.96	269
	6	77.16	25	57.72	18	74.65	23	70.98	66
	8	66.39	23	54.09	22	69.00	19	62.94	64
H5	1	103.98	118	94.89	107	90.86	107	96.82	332
	2	99.95	244	91.09	228	91.58	210	94.41	682
	3	104.78	121	93.99	93	92.82	89	95.83	279
	4	103.05	166	102.19	171	87.71	143	98.17	480
	5	103.77	100	95.20	87	90.18	82	96.86	269
	6	101.72	25	93.90	18	93.04	23	96.56	66
	8	83.54	24	85.24	22	88.40	20	85.58	66
H6	1	153.58	118	141.63	141	121.38	110	139.21	337
	2	148.34	245	138.67	138	123.16	214	137.29	688
	3	154.08	121	144.05	94	127.38	89	140.36	280
	4	155.11	167	152.61	174	120.48	145	143.38	486
	5	152.89	99	144.22	88	122.28	82	140.72	269
	6	151.56	25	142.80	18	126.65	23	140.49	66
	8	126.46	24	129.93	22	115.00	21	124.01	67
INC1	1	24.89	118	35.15	106	18.60	107	26.14	331
	2	24.18	241	33.17	227	18.77	206	25.55	674
	3	25.00	119	35.03	93	19.73	88	26.26	276
	4	25.97	165	37.31	169	19.34	141	28.03	475
	5	25.62	100	35.66	87	19.27	81	26.96	268
	6	24.56	25	36.18	18	18.39	23	25.58	66
	8	19.87	23	31.15	22	19.36	19	23.60	64
INC2	1	49.60	118	47.71	107	33.10	107	43.72	332
	2	48.66	244	47.90	228	33.25	210	43.66	682
	3	49.30	121	[illegible]	93	34.56	89	44.52	279
	4	51.71	166	[illegible]	171	33.78	143	45.94	480
	5	48.63	99	50.04	87	32.10	82	44.03	268
	6	49.84	25	48.90	18	33.61	23	43.93	66
	8	42.92	24	44.69	22	30.15	20	39.64	66
AINC	1	37.24	118	41.54	106	25.85	107	34.94	331
	2	36.52	241	40.55	227	26.07	206	34.68	674
	3	37.28	119	42.56	93	27.16	88	35.46	276
	4	38.86	165	44.02	169	26.63	141	37.06	475
	5	37.18	99	42.85	87	25.78	81	35.57	267
	6	37.20	25	42.54	18	26.00	23	34.75	66
	8	31.93	23	37.92	22	24.92	19	31.91	64

Appendix 2

TRAIT	POPULATION	A		B		C		ACROSS	
		Mean	N	Mean	N	Mean	N	Mean	N
TINC	1	74.49	118	83.07	106	51.70	107	61.41	331
	2	72.90	242	80.93	228	52.15	206	64.25	676
	3	74.56	119	85.02	94	54.33	88	62.62	277
	4	77.71	165	88.27	170	53.25	141	62.68	476
	5	74.35	99	85.08	88	51.56	81	63.15	268
	6	74.40	25	85.08	18	52.00	23	64.96	66
	8	63.87	23	75.84	22	49.84	19	63.82	64
D1	1	3.74	118	3.87	110	3.25	107	3.62	335
	2	3.79	246	3.85	231	3.35	209	3.68	686
	3	3.71	120	4.09	94	3.25	89	3.67	279
	4	3.88	167	4.21	174	3.20	143	3.80	484
	5	3.73	99	3.86	89	3.21	82	3.62	270
	6	3.72	25	3.66	19	3.38	23	3.58	67
	8	3.40	23	3.56	22	3.26	19	3.41	64
D2	1	3.10	118	3.19	110	2.65	107	2.98	335
	2	3.16	245	3.19	230	2.69	210	3.03	685
	3	3.07	120	3.36	94	2.60	89	3.00	279
	4	3.20	167	3.51	174	2.57	143	3.13	484
	5	3.12	99	3.25	89	2.61	82	3.01	270
	6	3.19	25	3.06	19	2.72	23	2.99	67
	8	2.82	23	3.01	22	2.71	19	2.85	64
MBL	1	40.57	118	46.70	110	28.98	100	39.09	328
	2	39.46	241	44.16	231	27.93	193	37.75	665
	3	40.57	119	46.96	94	27.74	86	38.40	275
	4	41.29	166	48.48	173	27.03	130	39.99	469
	5	40.19	98	46.28	89	26.79	75	38.39	262
	6	40.72	25	43.28	19	26.70	21	36.94	65
	8	35.76	24	45.41	22	28.14	19	36.80	65
MNL	1	56.41	119	60.08	110	49.46	110	55.35	339
	2	55.33	246	59.77	233	50.60	221	55.32	700
	3	55.85	122	60.92	93	51.93	88	56.61	279
	4	57.52	170	62.30	174	53.40	147	57.98	491
	5	53.99	100	60.85	89	52.85	83	55.89	272
	6	54.96	25	59.09	19	49.71	23	54.33	67
	8	49.59	25	58.33	22	43.11	22	50.31	69

Appendix 3: Range of population means and their percentage deviations from the general mean when population 4 and 7 were separated. Negative value means below the general mean.

Heights

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	H4	66.39	80.91	77.54	-14.38	4.35	17.07
	H5	83.54	104.78	101.97	-18.07	2.75	17.54
	H6	126.46	156.47	151.41	-16.48	3.34	16.08
B	H4	54.09	71.12	60.30	-10.30	17.94	23.51
	H5	85.24	109.23	95.02	-10.29	14.95	20.55
	H6	129.93	163.18	143.61	-9.52	13.63	19.28
C	H4	68.66	74.65	71.81	-4.39	3.95	23.82
	H5	87.46	93.04	90.59	-3.45	2.70	21.76
	H6	115.00	127.38	122.62	-6.21	3.88	22.56
ACROSS	H4	62.94	71.32	69.81	-9.84	2.16	21.15
	H5	85.58	98.78	95.89	-10.75	3.01	19.73
	H6	124.01	144.41	139.55	-11.13	3.48	18.96

CV -coefficient of variation

Height increments

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	INC1	19.87	26.18	24.85	-20.00	5.35	24.85
	INC2	42.92	51.79	49.39	-13.10	4.83	19.97
	AINC	31.93	39.01	37.20	-14.17	4.87	18.26
	TINC	63.87	78.01	74.36	-14.11	4.91	18.32
B	INC1	31.15	38.11	34.98	-10.95	8.95	24.54
	INC2	44.69	53.95	48.97	- 8.74	10.19	21.52
	AINC	37.92	46.03	42.01	-9.73	9.57	19.74
	TINC	75.84	92.06	83.94	-9.64	9.67	19.98
C	INC1	17.40	19.72	19.05	-8.66	3.52	32.30
	INC2	28.55	34.63	33.29	-14.24	4.02	30.40
	AINC	22.97	27.23	26.23	-12.43	3.81	26.17
	TINC	45.95	54.46	52.46	-12.41	3.81	26.17
ACROSS	INC1	23.60	28.13	26.40	-10.61	6.55	26.72
	INC2	39.64	46.00	44.22	-10.36	4.02	23.06
	AINC	31.91	37.15	35.38	-9.81	5.00	20.78
	TINC	63.82	74.43	70.73	-9.78	5.23	20.90

Appendix 3

Diameters

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	D1	3.40	3.95	3.77	-9.81	4.77	20.67
	D2	2.82	3.25	3.13	-9.90	3.83	21.46
B	D1	3.56	4.44	3.96	-10.10	12.12	22.52
	D2	3.01	3.82	3.29	-8.51	16.11	23.33
C	D1	3.17	3.39	3.27	-3.06	3.67	20.85
	D2	2.49	2.72	2.64	-5.68	3.03	22.06
ACROSS	D1	3.41	3.81	3.68	-7.34	3.53	21.57
	D2	2.85	3.13	3.03	-5.94	3.30	22.51

Branch and needle length

SITE	TRAIT	LOW.	HIGH.	MEAN	% OF MEAN		CV
					LOW.	HIGH.	
A	MBL	35.76	41.53	40.19	-11.02	3.33	18.14
	MNL	49.57	57.06	55.67	-10.96	2.50	15.42
B	MBL	43.28	49.75	46.17	-6.26	7.75	22.33
	MNL	58.33	60.92	60.63	-2.97	0.48	13.87
C	MBL	25.09	28.98	27.71	-9.45	4.58	27.26
	MNL	43.11	53.91	51.18	-15.77	5.33	18.16
ACROSS	MBL	36.80	40.12	38.56	-4.56	4.04	22.14
	MNL	50.31	58.34	55.96	-10.10	4.25	15.68

Appendix 4: Percentages of variance components at individual sites for data without family structure when population 4 and 7 were separated.

Heights

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	H4	1.19	2.79	5.79	90.22
	H5	1.82	2.90	7.25	88.03
	H6	2.69	2.85	6.85	87.60
B	H4	0.14	5.19	1.76	92.91
	H5	0.81	5.14	2.02	92.02
	H6	1.71	3.65	4.00	90.63
C	H4	2.74	0.00	2.20	95.06
	H5	3.05	0.00	4.19	92.75
	H6	2.28	0.00	6.29	91.43

Height increments

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	INC1	5.02	2.15	2.63	90.19
	INC2	2.90	1.37	3.36	92.37
	AINC	5.07	2.15	2.84	89.93
	TINC	5.09	2.19	2.87	89.85
B	INC1	1.63	3.01	1.93	93.42
	INC2	5.40	0.53	3.69	90.37
	AINC	4.14	1.82	4.89	89.15
	TINC	3.74	1.86	5.27	89.12
C	INC1	2.48	0.00	3.39	94.13
	INC2	0.17	0.00	6.97	92.86
	AINC	1.32	0.00	7.96	90.71
	TINC	1.32	0.00	7.96	90.71

Diameters

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	D1	6.76	0.14	5.75	87.34
	D2	6.26	0.00	5.28	88.45
B	D1	7.29	1.93	5.68	85.10
	D2	7.96	2.17	4.77	85.09
C	D1	2.57	0.00	5.35	92.08
	D2	4.38	0.00	8.25	87.37

Appendix 4

Branch and needle lengths

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	σ^2_e
A	MBL	5.09	0.33	4.68	89.90
	MNL	0.94	1.67	4.93	92.45
B	MBL	5.43	0.84	5.56	88.16
	MNL	7.62	0.71	2.96	88.70
C	MBL	1.70	0.00	4.94	93.37
	MNL	11.13	3.56	1.12	84.19

Appendix 5: Percentages of variance components across test sites for data without family structure when population 4 and 7 were separated.

Heights

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
H4	23.86	1.19	0.00	1.61	2.46	70.88
H5	5.99	1.88	0.36	1.81	4.30	85.65
H6	20.51	1.87	0.86	0.53	4.60	71.62

Height increments

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
INC1	54.06	1.36	0.69	0.22	1.12	42.55
INC2	41.20	1.78	0.52	0.00	2.73	53.75
AINC	50.64	1.89	0.74	0.00	2.53	44.20
TINC	50.21	1.84	0.79	0.00	2.63	44.54

Diameters

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
D1	13.04	5.56	0.00	0.72	4.59	76.09
D2	15.59	5.67	0.00	0.79	4.57	73.39

Branch and needle length

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	σ^2_e
MBL	50.37	2.34	0.18	0.004	2.52	44.58
MNL	18.75	5.39	1.93	0.00	2.49	71.44

Appendix 6: Hypotheses testing for the population and popuation x replication interaction effects for data without family structure when population 4 and 7 were pooled.

Heights

SITE	TRAIT	POPULATION			REPLICATION X POPULATION		
		DF V_1, V_2	F	SIGNIFICANCE	DF	F	SIGNIFICANCE
A	H4	6, 23.96	1.457	NS	24, 723	2.593	0.000
	H5	6, 23.96	1.785	NS	24, 723	2.634	0.000
	H6	6, 23.95	1.968	NS	24, 723	2.432	0.000
B	H4	6, 23.63	4.532	0.003	24, 683	1.234	NS
	H5	6, 23.70	4.512	0.003	24, 683	1.532	0.050
	H6	6, 23.72	3.276	0.017	24, 683	1.677	0.023
C	H4	6, 22.95	1.506	NS	24, 580	1.225	NS
	H5	6, 23.15	0.887	NS	24, 580	1.520	NS
	H6	6, 23.38	0.470	NS	24, 580	2.085	0.002

V_1 and V_2 -degrees of freedom in the numerator and denominator, respectively.

Height increments

SITE	TRAIT	POPULATION			REPLICATION X POPULATION		
		DF V_1, V_2	F	SIGNIFICANCE	DF	F	SIGNIFICANCE
A	INC1	6, 23.92	3.278	0.017	24, 723	1.528	NS
	INC2	6, 23.93	1.902	NS	24, 723	1.683	0.022
	AINC	6, 23.93	3.001	0.025	24, 723	1.642	0.028
	TINC	6, 23.93	3.001	0.025	24, 723	1.642	0.028
B	INC1	6, 23.68	3.047	0.023	24, 683	1.876	0.007
	INC2	6, 23.70	1.240	NS	24, 683	1.542	0.048
	AINC	6, 23.75	1.914	NS	24, 683	1.876	0.007
	TINC	6, 23.75	1.914	NS	24, 683	1.876	0.007
C	INC1	6, 22.85	0.178	NS	24, 580	1.124	NS
	INC2	6, 23.41	0.268	NS	24, 580	2.181	0.001
	AINC	6, 23.38	0.204	NS	24, 580	2.076	0.002
	TINC	6, 23.38	0.204	NS	24, 580	2.076	0.002

V_1 and V_2 -degrees of freedom in the numerator and denominator, respectively.

Appendix 6

Diameters

SITE	TRAIT	POPULATION			REPLICATION X POPULATION		
		DF V_1, V_2	F	SIGNIFICANCE	DF	F	SIGNIFICANCE
A	D1	6, 23.94	0.963	NS	24, 723	2.102	0.002
	D2	6, 23.94	1.003	NS	24, 723	2.007	0.003
B	D1	6, 23.81	1.712	NS	24, 683	2.480	0.000
	D2	6, 23.78	1.987	NS	24, 683	2.070	0.002
C	D1	6, 23.30	0.905	NS	24, 580	1.851	0.008
	D2	6, 23.40	0.842	NS	24, 580	2.157	0.001

V_1 and V_2 -degrees of freedom in the numerator and denominator, respectively.

Branch and needle lengths

SITE	TRAIT	POPULATION			REPLICATION X POPULATION		
		DF V_1, V_2	F	SIGNIFICANCE	DF	F	SIGNIFICANCE
A	MBL	6, 23.93	1.250	NS	24, 723	1.750	0.015
	MNL	6, 23.95	1.533	NS	24, 723	2.417	0.000
B	MBL	6, 23.80	1.259	NS	24, 683	2.345	0.000
	MNL	6, 23.66	1.388	NS	24, 683	1.373	NS
C	MBL	6, 23.35	0.521	NS	24, 580	1.999	0.003
	MNL	6, 22.38	5.690	0.001	24, 580	0.792	NS

V_1 and V_2 -degrees of freedom in the numerator and denominator, respectively.

Appendix 7: Hypotheses testing for the population and population x site interaction effects across sites for data without family structure when population 4 and 7 were pooled.

TRAIT	POPULATION			POPULATION X SITE		
	DF V_1, V_2	F	SIGNIFICANCE	DF	F	SIGNIFICANCE
H4	6, 11.91	0.847	NS	12, 71.28	2.343	0.014
H5	6, 11.91	1.361	NS	12, 71.37	2.118	0.026
H6	6, 11.87	2.215	NS	12, 71.42	1.353	NS
INC1	6, 11.83	3.280	0.038	12, 71.15	1.440	NS
INC2	6, 11.59	4.957	0.009	12, 71.34	0.456	NS
AINC	6, 11.75	4.766	0.010	12, 71.37	0.729	NS
TINC	6, 11.75	4.766	0.010	12, 71.37	0.729	NS
D1	6, 11.86	1.359	NS	12, 71.46	1.163	NS
D2	6, 11.88	1.019	NS	12, 71.42	1.365	NS
MBL	6, 11.81	1.656	NS	12, 71.44	0.871	NS
MNL	6, 11.77	5.116	0.008	12, 71.22	0.970	NS

V_1 and V_2 -degrees of freedom in the numerator and denominator, respectively.

Appendix 8: Hypotheses testing for the site effect for data without family structure when population 4 and 7 were pooled

TRAIT	DF V_1, V_2	F	SIGNIFICANCE
H4	2, 12.39	38.435	0.000
H5	2, 13.21	6.657	0.010
H6	2, 11.30	25.346	0.000
INC1	2, 12.59	125.071	0.000
INC2	2, 6.92	94.904	0.000
AINC	2, 9.18	100.516	0.000
TINC	2, 9.18	100.516	0.000
D1	2, 11.85	10.136	0.003
D2	2, 12.76	10.682	0.002
MBL	2, 10.10	91.732	0.000
MNL	2, 11.41	16.167	0.001

V_1 and V_2 -degrees of freedom in the numerator and denominator, respectively.

Appendix 9: Differences (cm) between individual population means and the general site means for heights and diameters for data without family structure.

SITE	POPULATION	H4	H5	H6	D1	D2
A	1	2.65	3.87	4.72	0.03	0.00
	2	-0.24	-0.16	-0.52	0.08	0.06
	3	4.47	4.68	5.22	0.01	-0.03
	4	0.77	2.94	6.25	0.17	0.11
	5	1.71	3.66	4.03	0.02	0.02
	6	0.72	1.61	2.70	0.01	0.09
	8	-10.05	-16.57	-22.40	-0.31	-0.28
B	1	1.16	1.10	-0.36	0.00	-0.04
	2	-1.15	-2.70	-3.32	-0.02	-0.04
	3	-0.12	0.20	2.06	0.22	0.14
	4	6.60	8.40	10.62	0.35	0.28
	5	-0.01	1.41	2.23	0.00	0.02
	6	-1.43	0.11	0.81	-0.21	-0.17
	8	-5.06	-8.55	-12.06	-0.31	-0.21
C	1	0.50	0.20	-0.95	-0.02	0.00
	2	1.37	0.92	0.83	0.08	0.05
	3	0.82	2.16	5.05	-0.02	-0.05
	4	-2.65	-2.95	-1.85	-0.07	-0.08
	5	-0.14	-0.48	-0.05	-0.05	-0.03
	6	2.89	2.38	4.32	0.11	0.07
	8	-2.76	-2.26	-7.33	-0.01	0.07

Appendix 10: Variance components and standard errors (E) at individual sites. Zero represent negative variances

SITE	TRAIT	VARIANCE COMPONENT											
		σ^2_r	E	σ^2_p	E	σ^2_{rp}	E	$\sigma^2_{f(p)}$	E	$\sigma^2_{rf(p)}$	E	σ^2_w	E
A	H4	0.83	3.77	0.00	0.00	11.24	8.98	13.53	6.78	23.52	7.71	143.16	8.49
	H5	5.28	9.10	0.00	0.00	20.61	16.52	25.84	12.63	40.12	13.98	273.87	16.12
	H6	17.85	19.32	0.00	0.00	30.37	28.05	48.97	23.06	72.79	24.33	495.41	27.19
	INC1	2.23	1.67	0.00	0.00	0.52	1.32	1.61	1.16	5.21	1.76	33.36	1.98
	INC2	4.08	3.22	0.00	0.00	0.47	3.42	6.00	3.35	13.76	4.22	74.56	4.42
	AINC	2.95	2.16	0.00	0.00	0.45	1.76	2.94	1.67	7.38	2.15	35.93	2.14
	TINC	11.77	8.60	0.00	0.00	1.86	7.04	11.75	6.69	29.45	8.57	143.56	8.55
	MBL	3.12	2.41	0.00	0.00	2.25	2.20	4.02	1.86	4.36	1.94	42.11	2.51
	MNL	2.17	6.29	0.00	0.00	0.63	2.61	4.80	2.53	9.99	3.04	53.96	3.18
B	H4	0.00	0.00	3.92	5.28	2.41	7.66	11.68	6.92	24.14	9.13	166.81	11.57
	H5	2.84	11.57	11.37	11.01	3.09	13.12	9.87	10.76	61.12	19.12	309.48	19.29
	H6	10.31	21.90	9.97	11.18	23.81	30.45	20.16	21.48	122.54	37.11	619.06	38.35
	INC1	0.97	2.05	1.67	1.78	0.80	2.36	1.74	1.89	8.02	3.40	66.34	4.15
	INC2	5.74	4.59	0.00	1.23	2.19	4.42	3.07	3.38	20.27	6.00	92.23	5.76

Zero stands for negative variance components.

Appendix 10

SITE	TRAIT	VARIANCE COMPONENT											
		σ^2_r	E	σ^2_p	E	σ^2_{rp}	E	$\sigma^2_{f(p)}$	E	$\sigma^2_{rf(p)}$	E	σ^2_w	E
	AINC	2.66	6.63	0.26	1.27	2.02	2.92	1.94	2.11	12.60	3.75	57.69	3.61
	TINC	10.03	10.56	1.21	5.36	10.22	12.11	7.29	8.29	49.39	14.90	233.72	14.58
	MBL	3.89	3.98	0.12	1.59	5.63	4.27	0.00	0.00	16.65	4.91	74.79	4.68
	MNL	6.82	4.41	0.45	0.97	0.00	0.00	2.21	1.80	6.70	2.90	58.49	3.61
C	H4	8.46	7.04	0.00	0.00	0.00	0.00	22.42	11.81	33.80	13.91	240.04	15.86
	H5	12.58	12.23	0.00	0.00	15.07	17.92	32.00	15.35	33.16	16.37	305.15	20.10
	H6	24.52	25.07	0.00	0.00	41.38	35.30	47.32	25.86	67.20	31.90	604.15	39.36
	INC1	0.79	1.00	0.00	0.00	1.79	1.65	1.30	1.10	3.50	1.82	34.52	2.29
	INC2	0.06	2.07	0.00	0.00	8.65	5.42	5.68	3.28	5.37	4.56	92.92	6.12
	AINC	0.49	1.31	0.00	0.00	4.53	2.72	1.92	1.43	4.27	2.23	42.32	2.80
	TINC	1.85	5.05	0.00	0.00	16.93	10.59	8.17	5.86	16.45	8.94	173.02	11.43
	MBL	0.92	1.45	0.00	0.00	2.45	2.44	1.69	1.63	5.47	2.84	50.73	3.15
	MNL	11.12	7.27	1.09	1.59	1.90	2.57	1.98	1.88	2.74	3.37	81.98	5.25

Zero stands for negative variance components.

Appendix 10

SITE	TRAIT	VARIANCE COMPONENT											
		σ^2_r	E	σ^2_p	E	σ^2_{rp}	E	$\sigma^2_{f(p)}$	E	$\sigma^2_{rf(p)}$	E	σ^2_w	E
A	D1	0.047	0.034	0.00	0.00	0.025	0.024	0.021	0.017	0.081	0.027	0.52	0.031
	D2	0.035	0.024	0.00	0.00	0.012	0.015	0.012	0.011	0.052	0.019	0.38	0.023
B	D1	0.072	0.054	0.004	0.015	0.015	0.036	0.0048	0.024	0.27	0.058	0.58	0.034
	D2	0.057	0.040	0.00	0.00	0.0054	0.027	0.0102	0.021	0.203	0.042	0.41	0.025
C	D1	0.012	0.014	0.00	0.00	0.0201	0.023	0.025	0.017	0.085	0.027	0.40	0.026
	D2	0.022	0.018	0.00	0.00	0.016	0.017	0.017	0.013	0.063	0.019	0.27	0.018

Zero stands for negative variance components.

Appendix 11: Variance components and standard errors (E) across sites. Zero represent negative variances.

TRAIT	VARIANCE COMPONENT															
	σ^2_s	E	$\sigma^2_{r(s)}$	E	σ^2_p	E	σ^2_{sp}	E	$\sigma^2_{r(s)p}$	E.	$\sigma^2_{f(p)}$	E	$\sigma^2_{sf(p)}$	E	σ^2_e	E	σ^2_w	E
H4	72.69	52.59	3.61	4.21	0.00	0.00	0.00	0.00	5.47	10.54	2.77	3.68	11.59	5.42	30.27	6.26	189.73	7.17
H5	24.26	20.17	9.10	9.12	0.00	0.00	2.64	5.96	11.71	16.53	9.12	6.15	10.57	7.07	46.16	9.90	309.76	11.16
H6	178.56	131.24	23.37	18.62	0.00	0.00	0.00	8.65	28.42	33.67	12.64	11.48	27.99	15.19	92.49	19.23	595.78	21.35
INC1	62.18	44.30	1.45	2.18	0.45	0.69	0.033	0.47	1.19	1.27	0.20	0.35	0.00	0.00	6.38	1.46	46.94	1.70
INC2	75.03	53.62	3.82	2.75	0.18	0.58	0.00	0.00	3.36	4.89	2.18	1.69	3.35	2.09	12.96	2.85	90.30	3.26
AINC	59.45	42.45	2.38	2.00	0.34	0.51	0.00	0.00	2.47	2.64	1.45	0.89	0.75	0.97	8.25	1.61	47.03	1.70
TINC	238.96	170.58	9.59	8.21	1.69	2.11	0.00	0.00	9.84	10.78	5.81	3.61	3.40	4.00	33.57	6.54	190.85	6.90
MBL	78.16	56.03	4.11	2.67	0.104	0.54	0.00	0.00	3.44	3.23	1.42	1.05	1.21	4.30	9.34	2.09	65.68	2.40
MNL	18.21	14.03	6.78	3.74	0.62	0.82	0.00	0.00	0.48	3.25	2.52	1.16	0.00	0.00	7.84	1.98	69.51	2.47

Zero stands for negative variance components.

Appendix 11

TRAIT	VARIANCE COMPONENT															
	σ^2_s	E	$\sigma^2_{r(s)}$	E	σ^2_p	E	σ^2_{sp}	E	$\sigma^2_{r(s)p}$	E	$\sigma^2_{f(p)}$	E	$\sigma^2_{sf(p)}$	E	σ^2_e	E	σ^2_w	E
D1	0.12	0.092	0.048	0.025	0.0012	0.0033	0.00	0.00	0.013	0.023	0.00	0.00	0.019	0.015	0.16	0.023	0.52	0.019
D2	0.104	0.08	0.041	0.02	0.00012	0.0021	0.00	0.00	0.0095	0.018	0.00	0.00	0.016	0.012	0.12	0.017	0.38	0.013

Zero stands for negative variance components.

Appendix 12: Percentages of variance components at individual sites. Values for site A includes family 2914.

SITE	TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	$\sigma^2_{f(p)}$	$\sigma^2_{rf(p)}$	σ^2_w
A	H4	0.43	0.00	5.84	7.04	12.23	74.45
	H5	1.43	0.00	5.63	7.06	10.97	74.88
	H6	2.68	0.00	4.56	7.36	10.94	74.45
	INC1	5.19	0.00	1.21	3.75	12.14	77.71
	INC2	4.13	0.00	0.47	6.07	13.92	75.41
	AINC	5.94	0.00	0.91	5.92	14.86	72.37
	TINC	5.93	0.00	0.94	5.92	14.84	72.36
	D1	6.77	0.00	3.60	3.03	11.67	74.93
	D2	7.13	0.00	2.44	2.44	10.59	77.39
	MBL	5.58	0.00	4.03	7.20	7.80	75.38
	MNL	3.03	0.00	0.88	6.71	13.96	75.41
B	H4	0.00	1.88	1.15	5.59	11.55	79.83
	H5	0.71	2.86	0.78	2.48	15.36	77.80
	H6	1.28	2.24	2.95	2.50	15.21	76.82
	INC1	1.22	2.10	1.01	2.19	10.08	83.40
	INC2	4.65	0.00	1.77	2.49	16.41	74.68
	AINC	3.46	0.34	2.62	2.51	16.33	74.76
	TINC	3.22	0.39	3.28	2.34	15.84	74.94
	D1	7.61	0.43	1.59	0.51	28.54	61.32
	D2	8.31	0.00	0.79	1.49	29.61	59.80
	MBL	3.85	0.12	5.57	0.00	16.47	73.99
	MNL	9.13	0.60	0.00	2.96	8.97	78.33
C	H4	2.78	0.00	0.00	7.36	11.09	78.77
	H5	3.16	0.00	3.79	8.04	8.33	76.68
	H6	3.12	0.00	5.27	6.03	8.56	77.00
	INC1	1.88	0.00	4.27	3.10	8.35	82.39
	INC2	0.053	0.00	7.68	5.04	4.77	82.46
	AINC	0.91	0.00	8.46	3.59	7.98	79.06
	TINC	0.85	0.00	7.82	3.77	7.60	79.95
	D1	2.21	0.00	3.71	4.61	15.68	73.79
	D2	5.67	0.00	4.12	4.38	16.24	69.59
	MBL	1.50	0.00	4.00	2.76	8.93	82.81
	MNL	11.03	1.08	1.88	1.96	2.72	81.32

Appendix 13: Percentages of variance components at site A without family 2914

TRAIT	σ^2_r	σ^2_p	σ^2_{rp}	$\sigma^2_{f(p)}$	$\sigma^2_{rf(p)}$	σ^2_w
H4	0.61	0.00	6.05	4.20	13.28	75.86
H5	1.98	0.00	5.47	3.33	11.83	77.39
H6	3.50	0.00	4.74	4.81	12.14	74.79
INC1	5.89	1.18	1.04	0.86	12.29	78.72
INC2	4.41	0.00	0.61	5.65	13.97	75.36
AINC	6.52	0.42	1.16	4.29	14.88	72.81
TINC	6.49	0.39	1.17	4.30	14.85	72.78
D1	7.52	0.00	2.27	2.94	11.96	75.32
D2	7.43	0.00	1.85	2.01	10.98	77.74
MBL	6.53	0.00	3.51	6.29	7.69	75.98
MNL	3.11	0.00	0.80	6.36	14.59	75.13

Appendix 14: Percentages of variance components across sites. Family 2914 was excluded.

Sites A, B & C combined.

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	$\sigma^2_{f(p)}$	$\sigma^2_{sf(p)}$	σ^2_e	σ^2_w
H4	22.99	1.14	0.00	0.00	1.73	0.88	3.67	9.57	60.00
H5	5.73	2.15	0.00	0.62	2.77	2.15	2.50	10.90	73.17
H6	18.64	2.44	0.00	0.00	2.96	1.32	2.92	9.64	62.11
INC1	52.33	1.22	0.38	0.03	1.00	0.17	0.00	5.37	39.50
INC2	39.25	2.00	0.09	0.00	1.76	1.14	1.75	6.78	47.23
AINC	48.68	1.95	0.28	0.00	2.02	1.19	0.61	6.76	38.51
TINC	48.40	1.94	0.34	0.00	1.99	1.18	0.69	6.80	38.66
D1	13.62	5.45	0.14	0.00	1.14	0.00	2.16	18.16	59.01
D2	15.51	6.11	0.02	0.00	1.42	0.00	2.39	17.89	56.66
MBL	47.81	2.51	0.06	0.00	2.10	0.87	0.74	5.71	40.18
MNL	17.52	6.52	0.60	0.00	0.46	2.42	0.00	7.54	66.86

Sites A & C combined.

TRAIT	σ^2_s	$\sigma^2_{r(s)}$	σ^2_p	σ^2_{sp}	$\sigma^2_{r(s)p}$	$\sigma^2_{f(p)}$	$\sigma^2_{sf(p)}$	σ^2_e	σ^2_w
H4	4.45	1.97	0.00	0.00	2.43	3.38	2.24	12.17	73.35
H5	11.49	2.71	0.00	0.00	3.76	3.33	1.87	8.78	68.05
H6	31.82	2.52	0.00	0.00	3.33	1.77	2.35	7.05	51.17
INC1	23.88	2.87	0.03	0.00	1.77	0.18	0.81	9.82	60.62
INC2	51.75	1.21	0.02	0.00	1.82	1.49	1.41	4.33	37.96
AINC	49.76	2.08	0.00	0.00	2.23	1.20	1.05	5.77	37.91
TINC	49.49	2.01	0.04	0.00	2.13	1.18	1.12	5.63	38.39
D1	16.25	5.00	0.00	0.00	2.50	1.25	1.25	12.50	61.25
D2	19.67	4.92	0.00	0.00	1.64	1.64	0.00	13.11	59.02
MBL	52.62	2.12	0.00	0.00	1.39	1.52	0.59	3.29	38.46
MNL	8.51	6.69	0.32	0.07	1.09	1.97	1.02	8.50	71.61

Appendix 15: Hypotheses testing with family structure for site A. Values include family 2914.

Height 4 (H4)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 14.08	0.714	NS
Pop.	4, 22.84	0.463	NS
Rep. x Pop.	16, 98.55	2.276	0.007
Fam (Pop.)	25, 97.64	2.193	0.003
Rep. x Fam (Pop.)	100, 538.00	1.674	0.000
Error	538.00,		

Height 5 (H5)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 14.07	1.292	NS
Pop.	4, 23.22	0.418	NS
Rep. x Pop.	16, 98.73	2.258	0.008
Fam (Pop.)	25, 97.74	2.266	0.002
Rep. x Fam (Pop.)	100, 538.00	1.750	0.000
Error	538.00		

Height 6 (H6)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 13.67	2.286	NS
Pop.	4, 23.34	0.440	NS
Rep. x Pop.	16, 98.92	1.860	0.033
Fam (Pop.)	25, 97.82	2.420	0.001
Rep. x Fam (Pop.)	100, 538.00	1.814	0.000
Error	538.00		

Height increment 1(INC1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.60	4.605	0.016
Pop.	4, 17.31	0.864	NS
Rep. x Pop.	16, 98.14	1.256	NS
Fam (Pop.)	25, 98.14	1.741	0.029
Rep. x Fam (Pop.)	100, 538.00	1.609	0.001
Error	538.00		

Appendix 15

Height increment 2 (INC2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.46	5.459	0.011
Pop.	4, 16.32	0.777	NS
Rep. x Pop.	16, 98.69	0.920	NS
Fam (Pop.)	25, 97.87	1.963	0.010
Rep. x Fam (Pop.)	100, 538.00	1.856	0.000
Error	538.00		

Mean height increment (AINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.90	6.580	0.005
Pop.	4, 17.89	0.852	NS
Rep. x Pop.	16, 98.84	1.027	NS
Fam (Pop.)	25, 97.93	2.095	0.005
Rep. x Fam (Pop.)	100, 538.00	1.905	0.000
Error	538.00		

Total height increment (TINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.90	6.580	0.005
Pop.	4, 17.89	0.852	NS
Rep. x Pop.	16, 98.84	1.027	NS
Fam (Pop.)	25, 97.93	2.095	0.005
Rep. x Fam (Pop.)	100, 538.00	1.905	0.000
Error	538.00		

Diameter 1 (D1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 13.49	4.584	0.016
Pop.	4, 17.52	0.567	NS
Rep. x Pop.	16, 98.21	1.728	0.054
Fam (Pop.)	25, 97.71	1.529	NS
Rep. x Fam (Pop.)	100, 538.00	1.725	0.000
Error	538.00		

Appendix 15

Diameter 2 (D2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 13.01	6.047	0.006
Pop.	4, 16.22	0.514	NS
Rep. x Pop.	16, 98.02	1.439	NS
Fam (Pop.)	25, 97.58	1.485	NS
Rep. x Fam (Pop.)	100, 538.00	1.634	0.000
Error	538.00		

Mean branch length (MBL)

SOURCE	DF	F	SIGNIFICANCE
Rep.	4, 13.05	5.710	0.007
Pop.	4, 22.21	0.292	NS
Rep. x Pop.	16, 98.37	1.465	NS
Fam (Pop.)	25, 97.34	2.479	0.001
Rep. x Fam (Pop.)	100, 538.00	1.485	0.003
Error	538.00		

Mean needle length (MNL)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.56	3.227	0.048
Pop.	4, 19.40	0.723	NS
Rep. x Pop.	16, 98.85	1.239	NS
Fam (Pop.)	25, 97.93	2.107	0.005
Rep. x Fam (Pop.)	100, 538.00	1.905	0.000
Error	538.00		

Appendix 16: Hypotheses testing with family structure for site B

Height 4 (H4)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.96	1.011	NS
Pop.	4, 17.60	1.680	NS
Rep. x Pop.	16, 92.57	1.235	NS
Fam (Pop.)	24, 91.77	1.887	0.017
Rep. x Fam (Pop.)	95, 505.00	1.644	0.000
Error	505.00		

Height 5 (H5)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.52	1.258	NS
Pop.	4, 15.37	2.405	NS
Rep. x Pop.	16, 92.37	1.433	NS
Fam (Pop.)	24, 91.97	1.431	NS
Rep. x Fam (Pop.)	95, 505.00	1.754	0.000
Error	505.00		

Height 6 (H6)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.70	1.845	NS
Pop.	4, 15.58	1.617	NS
Rep. x Pop.	16, 92.65	1.526	NS
Fam (Pop.)	24, 92.19	1.412	NS
Rep. x Fam (Pop.)	95, 505.00	1.892	0.000
Error	505.00		

Height increment 1(INC1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.05	2.071	NS
Pop.	4, 13.88	2.327	NS
Rep. x Pop.	16, 91.42	1.263	NS
Fam (Pop.)	24, 91.35	1.357	NS
Rep. x Fam (Pop.)	95, 505.00	1.451	0.006
Error	505.00		

Appendix 16

Height increment 2 (INC2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.09	4.146	0.025
Pop.	4, 14.16	0.572	NS
Rep. x Pop.	16, 92.70	1.287	NS
Fam (Pop.)	24, 92.26	1.371	NS
Rep. x Fam (Pop.)	95, 505.00	1.938	0.000
Error	505.00		

Mean height increment (AINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.53	3.061	NS
Pop.	4, 14.29	1.135	NS
Rep. x Pop.	16, 92.63	1.455	NS
Fam (Pop.)	24, 92.27	1.297	NS
Rep. x Fam (Pop.)	95, 505.00	1.943	0.000
Error	505.00		

Total height increment (TINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.53	3.064	NS
Pop.	4, 14.30	1.135	NS
Rep. x Pop.	16, 92.63	1.455	NS
Fam (Pop.)	24, 92.27	1.298	NS
Rep. x Fam (Pop.)	95, 505.00	1.943	0.000
Error	505.00		

Diameter 1 (D1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.26	4.615	0.017
Pop.	4, 10.01	1.250	NS
Rep. x Pop.	16, 93.85	1.335	NS
Fam (Pop.)	24, 93.43	0.928	NS
Rep. x Fam (Pop.)	95, 505.38	3.389	0.000
Error	505.00		

Appendix 16

Diameter 2 (D2)

SOURCE	DF	F	SIGNIFICANCE
	V_1, V_2		
Rep.	4, 11.56	6.190	0.006
Pop.	4, 10.72	1.277	NS
Rep. x Pop.	16, 94.03	1.114	NS
Fam (Pop.)	24, 93.41	1.117	NS
Rep. x Fam (Pop.)	95, 550.00	3.350	0.000
Error	505.00		

Mean branch length (MBL)

SOURCE	DF	F	SIGNIFICANCE
	V_1, V_2		
Rep.	4, 13.39	3.316	0.044
Pop.	4, 14.86	1.019	NS
Rep. x Pop.	16, 92.59	1.954	0.025
Fam (Pop.)	24, 92.31	1.196	NS
Rep. x Fam (Pop.)	95, 505.00	1.979	0.000
Error	505.00		

Mean needle length (MNL)

SOURCE	DF	F	SIGNIFICANCE
Rep.	4, 11.10	11.951	0.001
Pop.	4, 14.79	1.221	NS
Rep. x Pop.	16, 91.92	1.009	NS
Fam (Pop.)	24, 91.46	1.689	0.040
Rep. x Fam (Pop.)	95, 505.00	1.498	0.003
Error			

Appendix 17

Appendix 16: Hypotheses testing with family structure for site C.

Height 4 (H4)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 9.83	4.780	0.020
Pop.	4, 14.68	0.649	NS
Rep. x Pop.	16, 89.29	0.757	NS
Fam (Pop.)	24, 84.12	2.062	0.008
Rep. x Fam (Pop.)	94, 412.00	1.664	0.000
Error	412.00		

Height 5 (H5)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.12	4.668	0.019
Pop.	4, 18.46	0.451	NS
Rep. x Pop.	16, 89.04	0.993	NS
Fam (Pop.)	24, 83.01	2.444	0.001
Rep. x Fam (Pop.)	94, 412.00	1.492	0.005
Error	412.00		

Height 6 (H6)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.89	2.948	NS
Pop.	4, 22.42	0.212	NS
Rep. x Pop.	16, 87.80	1.636	NS
Fam (Pop.)	24, 81.81	2.524	0.001
Rep. x Fam (Pop.)	94, 412.00	1.341	0.029
Error	412.00		

Height increment 1(INC1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.18	2.810	NS
Pop.	4, 9.97	0.205	NS
Rep. x Pop.	16, 87.11	1.006	NS
Fam (Pop.)	24, 84.67	1.138	NS
Rep. x Fam (Pop.)	94, 412.00	1.765	0.000
Error	412.00		

Appendix 17

Height increment 2 (INC2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 13.88	1.110	NS
Pop.	4, 23.30	0.218	NS
Rep. x Pop.	16, 82.67	2.451	0.004
Fam (Pop.)	24, 77.91	2.387	0.002
Rep. x Fam (Pop.)	94, 412.00	1.007	NS
Error	412.00		

Mean height increment (AINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 13.52	1.599	NS
Pop.	4, 19.46	0.320	NS
Rep. x Pop.	16, 85.13	2.081	0.016
Fam (Pop.)	24, 81.50	1.774	0.030
Rep. x Fam (Pop.)	94, 409.00	1.273	NS
Error	409.00		

Total height increment (TINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 13.51	1.602	NS
Pop.	4, 19.48	0.321	NS
Rep. x Pop.	16, 85.17	2.072	0.017
Fam (Pop.)	24, 81.52	1.779	0.029
Rep. x Fam (Pop.)	94, 409.00	1.275	NS
Error	409.00		

Diameter 1 (D1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.31	4.196	0.026
Pop.	4, 14.03	0.774	NS
Rep. x Pop.	16, 88.67	1.014	NS
Fam (Pop.)	24, 84.81	1.583	NS
Rep. x Fam (Pop.)	94, 412.00	1.792	0.000
Error	412.00		

Appendix 17

Diameter 2 (D2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.00	5.527	0.009
Pop.	4, 14.83	0.674	NS
Rep. x Pop.	16, 89.52	1.199	NS
Fam (Pop.)	24, 85.69	1.519	NS
Rep. x Fam (Pop.)	94, 412.00	1.986	0.000
Error	412.00		

Mean branch length (MBL)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 12.83	2.126	NS
Pop.	4, 17.88	0.310	NS
Rep. x Pop.	16, 85.11	1.581	NS
Fam (Pop.)	24, 81.53	1.708	0.039
Rep. x Fam (Pop.)	94, 412.00	1.310	0.040
Error	412.00		

Mean needle length (MNL)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Rep.	4, 11.39	12.151	0.001
Pop.	4, 7.60	2.036	NS
Rep. x Pop.	16, 82.14	1.019	NS
Fam (Pop.)	24, 81.01	0.923	NS
Rep. x Fam (Pop.)	94, 412.00	1.256	NS
Error	412.00		

Appendix 18: Hypotheses testing with family structure across sites when all three sites were included in analyses.

Height 4 (H4)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 7.89	48.645	0.000
Rep (Site)	12, 37.38	1.689	NS
Pop.	4, 8.87	0.284	NS
Site x Pop.	8, 42.41	1.134	NS
Rep (Site) x Pop.	48, 2.77.70	1.404	0.050
Fam (Pop.)	24, 47.00	1.347	NS
Site x Fam (Pop.)	48, 273.36	1.725	0.004
Rep (Site) x Fam (Pop.)	285, 1463.00	1.680	0.000
Within	1463.00		

Height 5 (H5)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 8.88	8.011	0.010
Rep (Site)	12, 38.88	1.907	NS
Pop.	4, 10.80	0.657	NS
Site x Pop.	8, 42.77	1.264	NS
Rep (Site) x Pop.	48, 277.13	1.634	0.008
Fam (Pop.)	24, 46.85	1.610	NS
Site x Fam (Pop.)	48, 273.34	1.498	0.025
Rep (Site) x Fam (Pop.)	285, 1463.00	1.677	0.000
Within	1463.00		

Height 6 (H6)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 8.11	27.912	0.000
Rep (Site)	12, 39.30	2.253	0.028
Pop.	4, 9.41	1.117	NS
Site x Pop.	8, 45.40	0.760	NS
Rep (Site) x Pop.	48, 277.65	1.725	0.004
Fam (Pop.)	24, 46.93	1.481	NS
Site x Fam (Pop.)	48, 273.53	1.603	0.011
Rep (Site) x Fam (Pop.)	285, 1463.00	1.704	0.000
Within	1463.00		

Appendix 18

Height increment 1 (INC1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 10.53	125.162	0.000
Rep (Site)	12, 35.82	2.937	0.006
Pop.	4, 12.34	1.859	NS
Site x Pop.	8, 25.10	1.347	NS
Rep (Site) x Pop.	48, 273.79	1.202	NS
Fam (Pop.)	24, 46.15	1.861	0.035
Site x Fam (Pop.)	48, 272.78	0.953	NS
Rep (Site) x Fam (Pop.)	285, 1463.00	1.598	0.000
Within	1463.00		

Height increment 2 (INC2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 6.66	88.307	0.000
Rep (Site)	12, 37.52	3.019	0.005
Pop.	4, 6.21	1.662	NS
Site x Pop.	8, 40.62	0.328	NS
Rep (Site) x Pop.	48, 276.57	1.434	0.040
Fam (Pop.)	24, 46.86	1.516	NS
Site x Fam (Pop.)	48, 272.91	1.547	0.017
Rep (Site) x Fam (Pop.)	285, 1463.00	1.616	0.000
Within	1463.00		

Mean height increment (AINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 7.98	100.167	0.000
Rep (Site)	12, 38.07	3.169	0.003
Pop.	4, 11.30	1.947	NS
Site x Pop.	8, 35.15	0.546	NS
Rep (Site) x Pop.	48, 276.68	1.503	0.024
Fam (Pop.)	24, 46.56	1.902	0.030
Site x Fam (Pop.)	48, 273.92	1.168	NS
Rep (Site) x Fam (Pop.)	285. 1463.00	1.765	0.000
Within	1463.00		

Appendix 18

Total height increment (TINC)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 7.98	100.121	0.000
Rep (Site)	12, 38.07	3.170	0.003
Pop.	4, 11.30	1.948	NS
Site x Pop.	8, 35.16	0.546	NS
Rep (Site) x Pop.	48, 276.68	1.503	0.024
Fam (Pop.)	24, 46.57	1.901	0.030
Site x Fam (Pop.)	48, 273.92	1.169	NS
Rep (Site) x Fam (Pop.)	285, 1463.00	1.765	0.000
Within	1463.00		

Diameter 1 (D1)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 10.94	9.467	0.004
Rep (Site)	12, 37.02	4.755	0.000
Pop.	4, 4.14	1.479	NS
Site x Pop.	8, 35.85	0.855	NS
Rep (Site) x Pop.	48, 279.26	1.347	NS
Fam (Pop.)	24, 46.89	0.826	NS
Site x Fam (Pop.)	48, 276.61	1.332	NS
Rep (Site) x Fam (Pop.)	285, 1463.00	2.336	0.000
Within	1463.00		

Diameter 2 (D2)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 11.45	9.866	0.004
Rep (Site)	12, 36.30	5.722	0.000
Pop.	4, 4.31	1.193	NS
Site x Pop.	8, 35.30	0.876	NS
Rep (Site) x Pop.	48, 279.56	1.261	NS
Fam (Pop.)	24, 46.94	0.865	NS
Site x Fam (Pop.)	48, 276.60	1.390	NS
Rep (Site) x Fam (Pop.)	285, 1463.00	2.331	0.000
Within	1463.00		

Appendix 18

Mean branch length (MBL)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 8.71	85.910	0.000
Rep (Site)	12, 39.80	3.392	0.002
Pop.	4, 10.42	1.253	NS
Site x Pop.	8, 40.92	0.609	NS
Rep (Site) x Pop.	48, 275.38	1.842	0.001
Fam (Pop.)	24, 46.61	1.655	NS
Site x Fam (Pop.)	48, 272.95	1.257	NS
Rep (Site) x Fam (Pop.)	285, 1463.00	1.622	0.000
Within	1463.00		

Mean needle length (MNL)

SOURCE	DF V_1, V_2	F	SIGNIFICANCE
Site	2, 11.22	13.705	0.001
Rep (Site)	12, 33.40	8.998	0.000
Pop.	4, 14.63	1.723	NS
Site x Pop.	8, 22.14	0.823	NS
Rep (Site) x Pop.	48, 274.70	0.997	NS
Fam (Pop.)	24, 46.24	2.506	0.004
Site x Fam (Pop.)	48, 272.51	1.014	NS
Rep (Site) x Fam (Pop.)	285, 1463.00	1.564	0.000
Within	1463.00		

Appendix 19: Deviations of family means from site means expressed as percentage of site means. NP = not planted.

Height at age 4 (H4).

FAMILY	SITE A	SITE B	SITE C
2901	4.56	0.93	-4.45
2902	-0.30	1.12	-6.23
2903	-6.90	12.69	-15.20
2904	8.85	10.16	6.32
2905	-5.63	9.77	-9.08
2906	0.47	12.10	5.35
2907	-2.17	-13.71	-3.94
2908	4.24	-14.12	1.29
2909	-3.24	4.12	-4.99
2910	3.78	10.97	5.04
2911	-7.27	4.03	-11.89
2912	5.47	5.27	4.72
2913	-2.96	-8.94	0.11
2914	16.76	NP	NP
2915	1.68	-6.17	10.41
2916	-5.40	3.59	-4.77
2917	-1.60	-3.66	-4.54
2918	4.00	-6.01	7.72
2919	-2.52	7.40	5.42
2920	-1.50	-5.69	-4.42
2921	-4.33	2.33	-5.99
2922	2.09	-16.31	11.30
2923	1.73	-9.10	0.23
2924	-15.92	-7.79	13.02
2925	-0.73	8.31	3.08
2926	6.04	15.71	16.53
2927	1.77	-6.80	7.59
2928	2.24	-8.31	-16.38
2929	5.42	-1.46	-5.73
2930	-8.39	-4.08	-3.72

Appendix 19.

Height at age 5 (H5).

FAMILY	SITE A	SITE B	SITE C
2901	5.51	1.52	-2.30
2902	0.79	6.23	-4.23
2903	-3.75	10.22	-14.56
2904	10.52	9.90	3.90
2905	-5.40	4.17	-7.17
2906	1.76	8.56	3.33
2907	0.95	-9.89	-9.50
2908	3.60	-5.90	3.86
2909	-3.71	3.13	-3.50
2910	2.55	10.11	6.87
2911	-9.05	-1.06	-8.67
2912	4.92	3.31	3.88
2913	-3.61	-5.27	-0.97
2914	19.17	NP	NP
2915	0.70	-4.46	12.09
2916	-8.10	1.98	-1.75
2917	0.60	1.03	-1.93
2918	1.47	-8.63	3.24
2919	-4.33	-7.21	4.12
2920	-3.21	0.26	-2.74
2921	-5.91	-4.42	-8.72
2922	2.74	-14.45	11.53
2923	1.57	-7.41	0.39
2924	-15.41	-7.84	10.76
2925	-0.76	4.13	2.08
2926	5.60	15.86	13.32
2927	0.94	-5.15	7.42
2928	1.92	-5.07	-14.18
2929	4.68	-1.96	-5.53
2930	-7.52	-3.93	-4.00

Appendix 19.

Height at age 6 (H6).

FAMILY	SITE A	SITE B	SITE C
2901	5.51	1.65	-2.86
2902	2.07	5.07	-1.81
2903	-3.92	9.07	-11.79
2904	11.75	4.99	3.76
2905	-4.37	4.17	-4.63
2906	3.81	6.14	5.04
2907	-0.58	-8.02	-9.13
2908	0.31	-5.95	1.34
2909	-2.07	4.17	0.27
2910	1.79	9.50	5.74
2911	-8.46	2.37	-2.89
2912	2.32	2.74	1.04
2913	-1.93	-1.92	1.99
2914	14.88	NP	NP
2915	0.70	-0.73	11.27
2916	-8.42	4.31	-6.34
2917	3.57	3.00	-4.11
2918	-3.00	-9.66	0.00
2919	-6.15	-5.28	2.56
2920	1.09	-1.17	-9.05
2921	-3.28	-7.30	-8.36
2922	3.81	-14.67	7.35
2923	2.61	-5.69	1.18
2924	-14.59	-6.77	13.67
2925	-0.66	4.93	3.13
2926	3.93	12.61	13.32
2927	-1.11	-4.08	7.10
2928	1.38	-5.66	-15.44
2929	3.55	-5.01	-3.43
2930	6.04	-4.22	-1.89

Appendix 19

Diameter 1 (D1).

FAMILY	SITE A	SITE B	SITE C
2901	9.56	3.44	-8.67
2902	-5.34	2.09	1.43
2903	-2.15	10.23	-6.24
2904	14.41	-2.63	0.79
2905	0.84	9.22	-0.82
2906	7.74	10.52	1.65
2907	-3.03	-12.19	-8.81
2908	4.38	-8.90	2.62
2909	-5.33	1.27	-1.12
2910	-5.67	7.18	-0.59
2911	-10.07	10.18	-2.42
2912	3.01	4.30	-5.05
2913	-5.01	-2.13	-6.91
2914	3.12	NP	NP
2915	-1.17	-0.37	12.43
2916	-6.49	2.79	-2.82
2917	5.33	-5.74	-2.57
2918	5.89	-10.76	-0.38
2919	-5.54	-3.83	3.97
2920	-5.12	3.29	-1.84
2921	-0.58	-4.04	-5.93
2922	5.33	-20.49	11.96
2923	8.71	-0.86	4.16
2924	-10.62	-0.46	10.72
2925	3.64	11.08	6.43
2926	-0.99	11.10	12.04
2927	-2.83	-11.71	4.99
2928	-1.64	-4.00	-23.31
2929	6.60	-4.79	1.52
2930	-8.31	-4.98	-3.12

Appendix 19

Diameter 2 (D2).

FAMILY	SITE A	SITE B	SITE C
2901	7.11	-2.67	-12.53
2902	-5.04	2.04	-3.28
2903	-3.00	10.28	-5.30
2904	12.96	-3.13	4.55
2905	0.90	10.67	-0.07
2906	6.22	12.54	3.65
2907	0.19	-10.09	-8.06
2908	5.78	-8.12	6.96
2909	-6.67	1.76	-2.63
2910	-3.31	9.41	0.03
2911	-10.98	10.06	-1.88
2912	1.33	4.19	-4.44
2913	-4.62	-3.29	-10.24
2914	4.89	NP	NP
2915	-3.44	-1.41	10.34
2916	-8.19	4.90	-3.75
2917	-1.21	-3.66	-3.68
2918	5.04	-10.21	1.19
2919	-3.87	-3.99	7.06
2920	-2.12	1.76	-1.16
2921	-0.72	-4.67	-8.37
2922	7.05	-19.38	8.99
2923	11.37	-2.28	1.12
2924	-7.54	-1.90	11.83
2925	4.63	9.32	5.40
2926	0.63	13.29	14.54
2927	-2.04	-10.35	2.10
2928	-1.59	-0.91	-17.61
2929	5.52	-11.20	3.90
2930	-7.80	-6.32	-2.78

Appendix 20: Family means and valid number of observations (N) on individual and across sites.

Height at age 4 (H4).

FAMILY	SITE A		SITE B		SITE C		ACROSS	
	MEAN	N	MEAN	N	MEAN	N	MEAN	N
2901	81.61	23	60.72	25	68.68	22	68.86	72
2902	77.82	22	60.83	24	67.40	15	68.87	63
2903	72.67	24	67.79	24	60.95	22	67.31	70
2904	84.96	25	66.27	22	76.42	19	76.27	66
2905	73.65	23	66.04	25	65.35	20	67.83	69
2906	78.42	24	67.44	25	75.73	22	73.72	71
2907	76.36	25	51.91	23	69.05	21	65.98	69
2908	81.36	25	51.67	15	72.81	21	71.11	61
2909	75.52	25	62.64	25	68.29	17	68.88	67
2910	81.00	24	66.76	25	75.50	22	73.80	72
2911	72.37	24	62.58	24	63.33	21	65.74	70
2912	82.32	25	63.33	24	75.27	22	73.72	71
2913	75.74	23	54.78	23	71.95	23	67.49	69
2914	91.13	23	NP	NP	NP	NP	NP	NP
2915	79.36	22	56.45	20	79.36	22	72.00	66
2916	73.83	24	62.32	25	68.45	22	66.22	74
2917	76.80	25	57.96	24	68.61	21	67.88	70
2918	81.17	23	56.54	24	77.43	21	70.16	68
2919	76.08	25	55.70	24	75.78	18	68.70	67
2920	76.88	25	56.74	23	68.71	17	68.44	64
2921	74.67	21	61.56	25	67.57	21	67.76	67
2922	79.68	25	50.35	20	80.00	20	71.61	66
2923	79.04	25	54.68	19	72.04	22	69.83	66
2924	65.62	24	55.47	19	81.24	21	67.73	64
2925	77.48	25	65.16	25	74.09	22	71.52	71
2926	82.76	21	69.61	23	83.76	21	78.43	65
2927	79.43	23	56.07	15	77.33	21	72.95	61
2928	79.80	25	55.16	19	60.10	19	66.43	63
2929	82.28	25	59.28	25	67.76	21	69.89	71
2930	71.50	24	57.71	24	69.21	24	66.14	72

Appendix 20.

Height at age 5 (H5).

FAMILY	SITE A		SITE B		SITE C		ACROSS	
	MEAN	N	MEAN	N	MEAN	N	MEAN	N
2901	108.56	23	96.47	24	89.09	22	97.36	72
2902	103.71	24	100.95	24	87.33	15	98.76	63
2903	99.04	24	104.74	25	77.91	23	95.08	71
2904	113.72	25	104.44	22	94.75	20	105.01	67
2905	97.35	23	98.99	25	84.65	20	93.47	69
2906	104.71	24	103.17	25	94.22	22	100.92	71
2907	103.88	25	85.63	23	82.52	21	92.11	68
2908	106.60	25	89.42	14	94.71	21	96.16	62
2909	99.08	25	98.00	25	88.00	17	95.86	67
2910	105.52	25	104.64	25	97.45	22	102.75	72
2911	93.58	24	94.02	24	83.28	21	89.88	70
2912	107.96	25	98.17	24	94.73	22	100.55	71
2913	99.18	22	90.02	23	90.30	23	93.15	69
2914	122.62	24	NP	NP	NP	NP	NP	NP
2915	103.62	24	90.79	21	102.21	23	99.94	69
2916	94.56	25	96.91	25	89.59	22	93.86	72
2917	103.52	25	96.01	24	89.42	21	96.72	70
2918	104.42	24	86.82	24	94.14	21	95.17	69
2919	98.44	25	88.18	24	94.94	18	94.71	68
2920	99.60	25	95.28	22	88.69	16	95.32	63
2921	96.82	22	90.83	25	83.24	21	90.42	68
2922	105.72	25	81.30	20	101.70	20	98.77	65
2923	104.52	25	87.99	19	91.54	22	94.47	67
2924	87.04	24	87.58	19	101.00	21	91.78	64
2925	102.12	25	98.95	25	93.09	22	98.26	72
2926	108.67	21	110.10	23	103.33	21	108.34	66
2927	103.87	23	90.13	15	97.95	22	98.27	60
2928	104.88	25	90.21	19	78.26	19	92.43	63
2929	107.72	25	93.17	25	86.14	21	96.21	71
2930	95.17	24	91.29	24	87.54	24	91.33	72

Appendix 20.

Height at age 6 (H6).

FAMILY	SITE A		SITE B		SITE C		ACROSS	
	MEAN	N	MEAN	N	MEAN	N	MEAN	N
2901	161.56	23	146.35	25	120.14	22	141.00	72
2902	156.30	23	151.28	24	121.43	16	145.90	63
2903	147.12	24	157.04	25	109.09	23	138.41	72
2904	171.12	25	151.16	24	128.32	22	151.32	71
2905	146.43	23	149.99	25	117.95	20	138.40	69
2906	158.96	24	152.82	25	129.91	22	147.79	71
2907	152.24	25	132.44	22	112.38	21	131.21	70
2908	153.60	25	135.42	15	125.33	21	137.76	62
2909	149.96	25	149.98	25	124.00	17	143.39	67
2910	155.87	24	157.66	25	130.77	22	147.70	72
2911	140.17	23	147.39	24	120.09	21	133.68	71
2912	156.68	25	147.93	24	124.95	22	143.89	71
2913	150.17	23	141.22	23	126.13	23	139.17	69
2914	175.92	24	NP	NP	NP	NP	NP	NP
2915	154.21	24	142.93	22	137.61	23	145.08	69
2916	140.24	25	150.18	25	115.82	23	134.64	74
2917	158.60	25	148.30	24	118.59	22	144.29	70
2918	148.54	24	130.07	24	123.67	21	133.55	70
2919	143.72	25	136.37	24	126.83	18	137.68	68
2920	154.79	24	142.29	23	112.47	19	140.13	65
2921	148.10	20	133.48	25	113.33	21	130.03	68
2922	158.96	25	122.85	20	132.76	21	140.66	67
2923	157.12	25	135.79	18	125.13	23	140.16	66
2924	130.78	23	134.23	19	140.57	21	134.64	64
2925	152.12	25	151.08	25	127.54	22	145.52	71
2926	159.14	21	162.13	23	140.14	21	155.20	66
2927	151.43	23	138.11	15	132.45	22	139.70	61
2928	155.24	25	135.82	20	104.58	19	134 13	64
2929	158.56	25	136.77	25	119.43	21	139.31	71
2930	143.87	24	137.90	25	121.33	24	134.42	73

Appendix 20.

Diameter 1 (D1).

FAMILY	SITE A		SITE B		SITE C		ACROSS	
	MEAN	N	MEAN	N	MEAN	N	MEAN	N
2901	4.15	23	4.10	25	2.98	22	3.73	71
2902	3.59	24	4.04	24	3.31	15	3.69	63
2903	3.71	24	4.36	25	3.06	23	3.73	72
2904	4.34	25	3.86	25	3.28	21	3.86	71
2905	3.82	23	4.32	25	3.23	21	3.79	70
2906	4.08	24	4.38	25	3.31	22	3.95	71
2907	3.67	24	3.48	23	2.97	22	3.43	70
2908	3.96	25	3.61	16	3.34	22	3.65	63
2909	3.59	25	4.01	25	3.22	17	3.65	67
2910	3.57	24	4.24	25	3.24	22	3.67	72
2911	3.41	24	4.36	25	3.18	21	3.68	70
2912	3.90	25	4.13	24	3.09	22	3.73	71
2913	3.60	23	3.87	23	3.03	23	3.50	69
2914	3.91	24	NP	NP	NP	NP	NP	NP
2915	3.74	24	3.94	22	3.66	23	3.78	69
2916	3.54	25	4.07	25	3.17	22	3.54	74
2917	3.99	25	3.73	25	3.18	21	3.66	71
2918	4.01	23	3.53	25	3.25	21	3.64	70
2919	3.58	25	3.81	25	3.39	19	3.64	68
2920	3.60	25	4.09	25	3.20	17	3.67	65
2921	3.77	22	3.80	25	3.07	21	3.60	67
2922	3.99	25	3.15	21	3.65	22	3.66	67
2923	4.12	25	3.93	19	3.39	23	3.82	67
2924	3.39	24	3.94	18	3.61	21	3.58	64
2925	3.93	25	4.40	25	3.47	23	3.94	73
2926	3.75	21	4.40	24	3.65	21	3.96	66
2927	3.68	23	3.50	16	3.42	22	3.54	61
2928	3.73	25	3.80	20	2.50	18	3.43	64
2929	4.04	25	3.77	25	3.31	21	3.73	71
2930	3.47	24	3.76	25	3.16	24	3.47	73

Appendix 20.

Diameter 2 (D2).

FAMILY	SITE A		SITE B		SITE C		ACROSS	
	MEAN	N	MEAN	N	MEAN	N	MEAN	N
2901	3.37	23	3.19	25	2.31	22	2.97	70
2902	2.99	23	3.35	23	2.55	15	3.03	63
2903	3.05	24	3.62	25	2.50	23	3.07	72
2904	3.56	24	3.18	25	2.76	20	3.19	71
2905	3.18	23	3.63	25	2.64	21	3.15	70
2906	3.34	24	3.69	25	2.74	22	3.28	71
2907	3.16	25	2.95	23	2.43	22	2.86	70
2908	3.33	25	3.01	16	2.82	21	3.08	62
2909	2.94	25	3.34	25	2.57	17	2.99	67
2910	3.04	24	3.59	25	2.64	22	3.08	72
2911	2.80	24	3.61	25	2.59	21	3.03	70
2912	3.19	25	3.42	24	2.52	22	3.06	71
2913	3.00	23	3.17	23	2.37	23	2.85	69
2914	3.30	24	NP	NP	NP	NP	NP	NP
2915	3.04	24	3.23	22	2.91	23	3.06	69
2916	2.89	25	3.44	25	2.54	22	2.89	75
2917	3.11	25	3.16	25	2.54	21	2.96	71
2918	3.31	23	2.94	25	2.67	21	3.01	70
2919	3.02	25	3.15	25	2.83	19	3.02	69
2920	3.08	24	3.34	23	2.67	17	3.04	65
2921	3.13	22	3.13	25	2.42	21	2.91	68
2922	3.37	25	2.64	20	2.88	22	2.99	67
2923	3.51	25	3.20	19	2.67	23	3.13	67
2924	2.91	24	3.22	18	2.95	21	3.01	63
2925	3.30	25	3.58	25	2.78	23	3.23	73
2926	3.17	20	3.71	24	3.02	21	3.29	66
2927	3.08	21	2.94	16	2.69	22	2.91	61
2928	3.10	25	3.25	20	2.17	16	2.87	64
2929	3.32	25	2.91	25	2.74	21	3.01	71
2930	2.90	24	3.07	25	2.57	24	2.85	73